THE FAMILY PTEROGENIIDAE, WITH NOTES ON THE PHYLOGENY OF THE HETEROMERA

John F. Lawrence

Museum of Comparative Zoology, Harvard University,
Cambridge, MA 02138

Abstract

The larva of *Pterogenius nietneri* Candeze and the larva and pupa of *Histanocerus pubescens* Motschulsky are described. The family Pterogeniidae is characterized on the basis of adult and larva. The Pterogeniidae are reviewed, with keys and descriptions of new species. A discussion is presented of some of the major adult and larval characters used in the classification of Heteromera, and comments are made on the major lineages. The phylogenetic position of the Pterogeniidae is discussed. The following species are described as new: *Pterogenius besucheti*, *Histanocerus fleaglei*, *H. minutus*, and *H. werneri*. The following new combinations are made: *Histanocerus abnormis* (Gebien) and *H. drescheri* (Pic).

Introduction

The family Pterogeniidae was proposed by Crowson (1955) for two peculiar genera from southeast Asia, *Pterogenius* Candeze and *Histanocerus* Motschulsky (= *Labidocera* Gebien). Crowson considered these beetles to be among the more primitive groups of Heteromera with a possible relationship to the Ciidae. The larva of *Pterogenius nietneri* was described by Candeze (1861), but the description was inadequate for phylogenetic purposes. I recently had the opportunity to study larvae of *P. nietneri*, as well as larvae and pupae of *Histanocerus pubescens* Motschulsky and larvae of at least one additional *Histanocerus* species. This paper includes larval and pupal descriptions, a recharacterization of the family Pterogeniidae based on adult and larval characters, a systematic review of the family with descriptions of new species, and a preliminary discussion of the morphology and evolution of the Heteromera and the relationship of the Pterogeniidae to other heteromerous families.

The terminology used in both larval and adult descriptions is discussed on pp. 44-52. In the *Histanocerus* key, TL refers to the combined lengths of elytra and pronotum (not the head), and EW refers to the greatest elytral width. Abbreviations used in the citation of specimens may be found in the acknowledgments (p. 54).

Descriptions of Immature Stages

Larva of *Pterogenius nietneri* Candeze

Body (Fig. 1) elongate, subcylindrical, slightly curved, lightly sclerotized except for head and abdominal apex, the latter bearing a pair of bifurcate urogomphi (Fig. 3). Vestiture of scattered, long setae. Length about 6mm.; width about 0.8mm.

Head (Figs. 2, 6) subglobular, somewhat quadrate in dorsal view, vertex slightly flattened; moderately sclerotized and yellowish-brown in color, with very fine and sparse punctation and very lightly impressed, reticulate microsculpture; vestiture of long setae. Epicranial stem about 0.33 × as long as head width, distinctly bent to left; frontal arms lyriform, sharply diverging anteriorly and extending to just behind antennal insertions, a broad, transverse ecdysial line connecting arms anteriorly; endocarina absent. Frontoclypeal area slightly flattened, produced forward in front of heavily sclerotized mandibular articulations, pigmented except for narrow apical band; frontoclypeal suture absent, but weakly impressed, transverse sulcus may be present between articulations. Epicranial halves without ventral ridges, the ventral mouthparts supported by hypostomal ridges about 0.33 × as long as head width; hypostomal rods very short. Ocelli 5 on each side, arranged as in Fig. 1, posterodorsal ocellus often lacking pigment and not easily visible. Labrum semicircular, only slightly wider than long, with 2 basal, 2 apical, and 4 lateral setae; tormae approximate and symmetrical; epipharynx as in Fig. 24, with 3 pairs of setae at apical edge, 2 pairs basolaterally, several very fine pegs mesally, and 2 larger ones near base; base of epipharynx bearing a dense cluster of posteromesally directed hairs, which grade into an asymmetrical, open ring of stout, flattened, pharyngeal spines, bordered laterally by several transverse, overlapping plates, fringed posteriorly by fine cuticular outgrowths; base of pharynx with an additional longitudinal, median series of short spines. Antenna (Fig. 7) about 0.2 × as long as head width, 3-segmented, segments about equal in length (1.2:1:1); segment 2 narrower than 1 and bearing sensory appendix which is about as long as 3 and ventral to it; 3 about 0.25 × as wide as 2 and bearing terminal seta which is almost 3 × its length. Antennal insertion partly concealed from above by a heavily sclerotized ridge, extending from dorsal mandibular articulation to hypostomal ridge, and separated from mouth cavity by a narrow bar. Gula well-developed, elongate, separated from submentum by suture, gular sutures converging anteriorly; tentorium consisting of 2 narrow, obliquely vertical apophyses, which converge apically but do not join.

Mandibles strongly asymmetrical, large and wedge-shaped, with triangular base and 2 apical teeth. Left mandible (Figs. 17, 20) with irregularly scalloped cutting edge, deeply incised basally; mola well-developed, elongate, parallel to long axis, and concave, with 2 distal teeth and about 15 transverse ridges alternating with rows of deep pits; dorsal surface with about 10 more or less parallel rows of very small cuticular processes, those in each row arranged 3 or 4 abreast and all facing basomesally. Right mandible (Figs. 16, 18, 19) with cutting edge interrupted, forming truncate process; mola somewhat larger and oblique, convex, with about 20 ridges; dorsal rows about 13. Both mandibles with basal patch of very small spines on ventral surface, and with 2 prominent setae on outer surface. Prostheca and basal lobe absent. Maxilla (Figs. 6, 25) free almost to base of mentum, mala about twice as long as wide, its apex obliquely truncate, bearing several spines and setae, a bifurcate uncus at inner third, and two subapical heavy spines at inner angle; dorsal surface with median row of setae extending to base of palpifer and an inner row of spines extending onto stipes; stipes elongate, its inner edge with a single isolated spine; cardo subtriangular, transverse, undivided externally, although partly divided by an internal ridge; articulating area elongate and oval, partly overlapping submentum and mentum; palp 3-segmented. Labium (Figs. 6, 8) with small, trapezoidal submentum, elongate mentum, short, quadrate prementum, and welldeveloped ligula bearing 2 setae at apex; palp 2-segmented. Hypopharyngeal sclerome consisting of transverse plate bearing 2 lateral wings (median portions of bracon), an asymmetrical, mola-like structure at apex of plate, 2 brushes of setae anterior to this, and another brush in its center.

Prothorax slightly longer than meso- or metathorax, tergum moderately pigmented at anterior end without transverse carina, with anterior and posterior row of long setae and scattered short setae; cervicosternum well-developed, bearing 2 setae, basisternum with 2 approximate setae near anterior end; coxal bases large and oval, separated by about 0.5 diameter. Meso- and metathoracic terga very lightly pigmented except for fine, transverse carina near anterior end, each with median, transverse row of long setae and anterior row of shorter ones; mesothoracic laterotergite bearing annular-biforous spiracle with accessory chambers facing dorsally and about as long as diameter of peritreme. Legs about equal in size and 0.75 × as long as thoracic width, each armed with a number of setae of varying lengths; coxa large and conical, anteriorly with 3 moderately long setae; femur slightly longer than tibia; tarsungulus with 2 setae of unequal lengths.

Abdomen about 1.8 × as long as thorax, segments 1 to 7 very lightly pigmented, each tergal plate with anterior carina, posterior row of longer setae, and anterior row of shorter ones; spiracles smaller than those of thorax, annular-biforous, with accessory chambers directed posterodorsally at a 45° angle, situated above the transverse laterotergites which bear 1 long and 2 or 3 shorter setae, more or less in a transverse row. Abdominal sterna with a single transverse row of long setae and several shorter setae. Tergum 8 more heavily pigmented, with anterior carina and 2 setal rows as in anterior segments, but with larger spiracle, whose accessory chambers form a slightly greater angle with the vertical axis. Tergum 9 (Fig. 3) lightly pigmented, except for pair of bifurcate urogomphi and a number of setiferous tubercles. Sterna 8 and 9 reduced in length, strongly transverse, each bearing a single row of setae. Segment 10 facing posteroventrally, tergum and sternum crescent shaped, with row of setae near apex; anus surrounded by 1 posterior and 5 anterior papillae, the lateral members of anterior group with outer patch of asperities.

Material examined. Series of about 25 specimens collected with adults by sifting in virgin forest near Hagkala, 1700-1800m, central CEYLON, Jan. 28, 1970, C. Besuchet and I. Löbl, coll. [MHNG]; 5 specimens collected with Berlese funnels at Kanda-ela Reservoir, 6200 ft., 5.6 mi. SW Nuwara Eliya, Northeast District, CEYLON, Feb. 10-12, 1970, D. Davis and W. Rowe [USNM]; 3 specimens collected with adults in polypore fungus at Peradeniya, CEYLON, 1910, Petch coll. [MCZC].
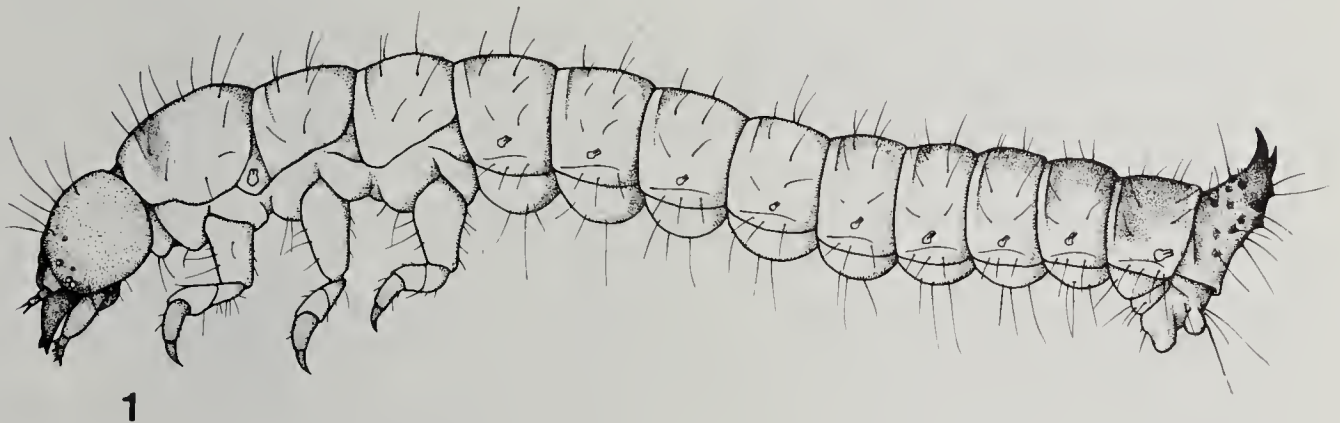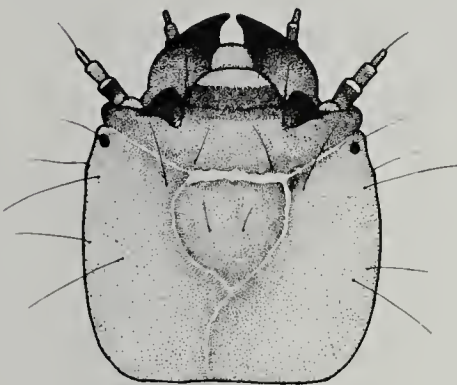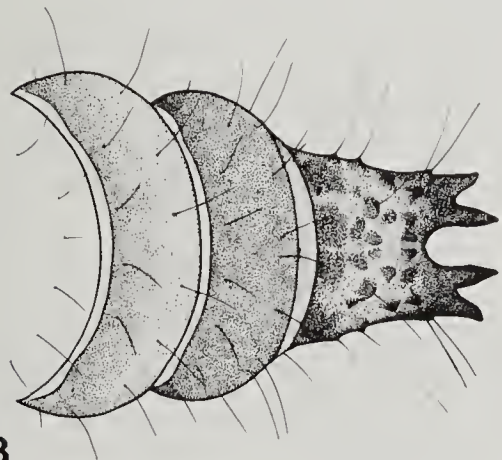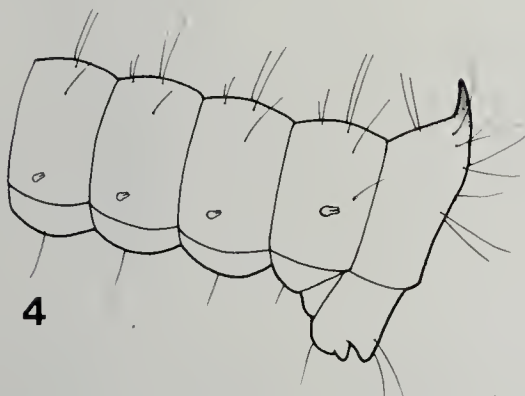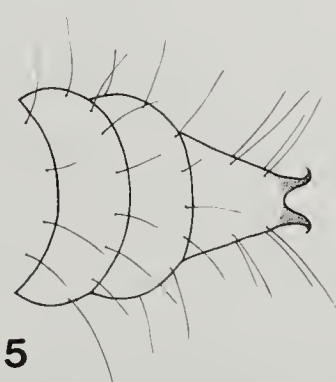

Figs. 1-3. *Pterogenius nietneri.* 1) Larva, lateral. 2) Larval head capsule, dorsal. 3) Larval abdominal apex, dorsal. Figs. 4-5. *Histanocerus pubescens.* 4) Larval abdominal apex, lateral. 5) Same, dorsal.

It should be noted that the two large spines at the inner apical angle of the mala are somewhat set off from the other apical armature and arise slightly below the apex. These could be interpreted as homologues of the spines borne on the laciniar lobe in Ciidae.
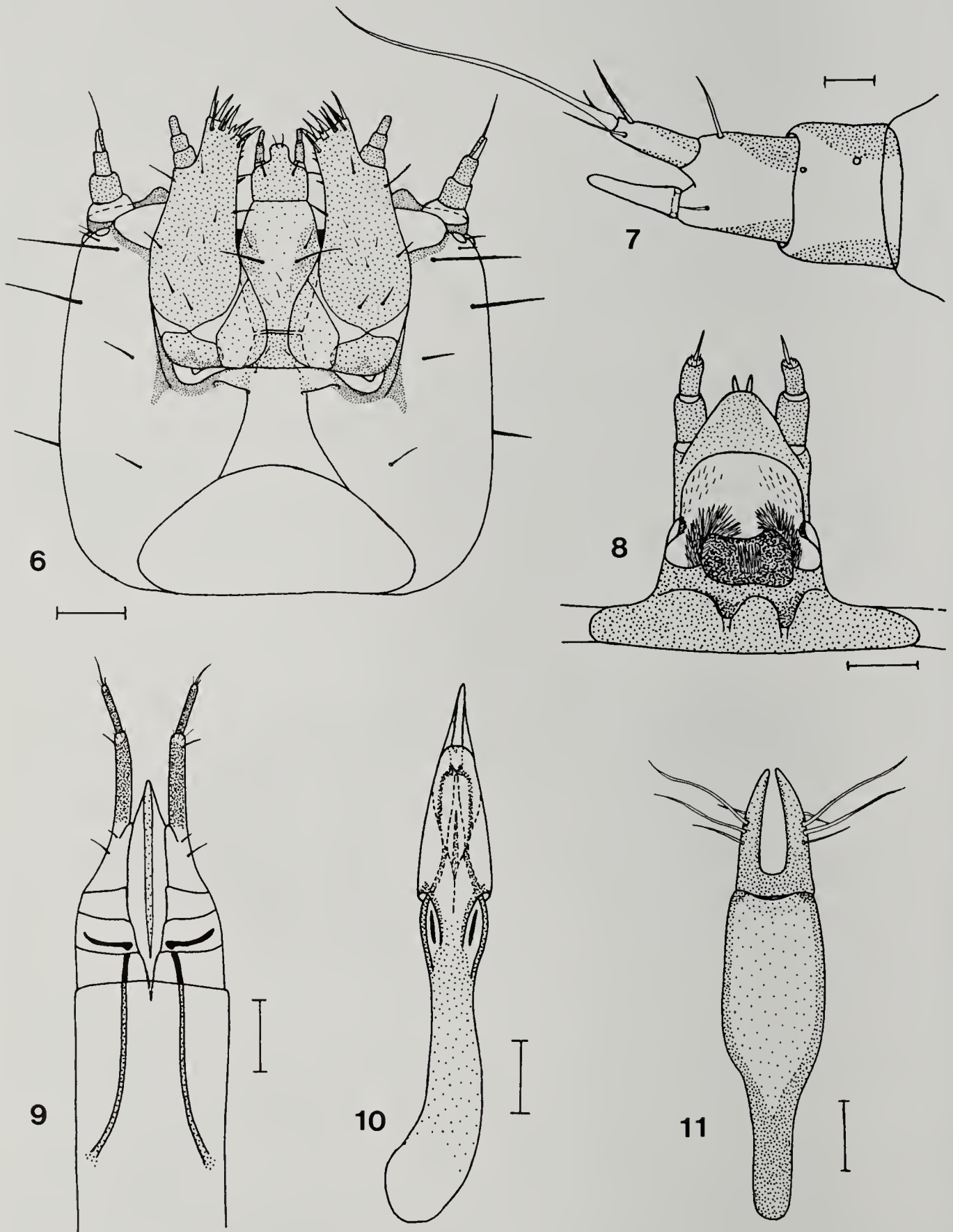
Figs. 6-11. *Pterogenius nietneri*. 6) Larval head capsule, ventral, mandibles and labrum removed. 7) Larval antenna, mesal. 8) Larval hypopharynx, dorsal. 9) Ovipositor, ventral. 10) Median lobe, ventral. 11) Tegmen, ventral. (1 line = 0.08mm. for 6; 0.06mm. for 7; 0.025mm. for 8; 0.125mm. for 9-11).

Larva of *Histanocerus pubescens* Motschulsky

Body more lightly sclerotized than that of *P. nietneri*, with simple, approximate urogomphi (Figs. 4-5). Length about 4mm.; width about 0.5mm. Details more or less as in *P. nietneri*, except as noted below.

Head yellowish in color; epicranial stem longer, about 0.4 × as long as head width, bent to left. Ocelli 4 on each side, arranged more or less as in *P. nietneri*, without reduced, posterodorsal ocellus. Antenna with sensory appendix distinctly longer than segment 3. Mandibles (Figs. 21-23) with fewer rows of dorsal cuticular processes; molar surface with finer transverse ridges and smaller pits between the ridges. Prothoracic tergum with pigment restricted to narrow anterior band, with distinct row of long setae at anterior end and a few short setae at posterior end. Meso- and metaterga and abdominal terga 1 to 8 devoid of pigment, each with transverse rows of longer and shorter setae. Legs shorter and broader than in *P. nietneri*, bearing short and stout setae or spines, each procoxa with a single, anteriorly projecting long seta. Tergum 9 (Figs. 4-5) unpigmented except for tips of urogomphi, which are simple and approximate, bearing a number of long setae.

Material examined. About 50 specimens collected with adults in the fruiting bodies of *Ganoderma* sp. in the Krau Game Reserve, Temerloh District, Pahang, MALAYSIA, Aug. 2, 1973, and Aug. 29, 1974, Lots 3484, 3717, and 3721 J. F. Lawrence (J. Fleagle, collector) [MCZC].

This larva and that of *Pterogenius* have an overall resemblance to those of Byturidae, Tetratomidae, Melandryidae, Ciidae, Colydiidae, and some clavicorn families such as Languriidae and Erotylidae. These are all relatively small forms, subcylindrical in cross-section, with distinct urogomphi, and a posteroventral, pygopod-like tenth segment, and they usually inhabit rotten wood or fungal fruiting bodies. Byturidae and the Clavicornia have a cylindrical, rather than transverse tenth segment and at least remnants of a mandibular prostheca. The distinctive head, with a bowed epicranial stem and transverse ecdysial line, the asymmetrical mandibles with a distinctive molar surface, and the enlarged 8th spiracle serve to distinguish pterogeniids from all of the above forms. Mycetophagid and archeocrypticid larvae have certain resemblances to pterogeniids, but in both groups the body is more flattened and the tenth segment more transverse and posteriorly oriented. The less flattened larvae in the pythid-salpingid group are easily distinguished by the presence of basal asperities on sternite 9.

The mandibles of pterogeniids are of a highly specialized, grinding type, analagous to the teeth of elephants. The numerous transverse molar ridges form multiple shearing surfaces used to cut reinforced polypore hyphae into small sections. The peculiarly bent epicranial stem may be associated with the distribution of muscle masses operating the highly asymmetrical mandibles.

Pupa of *Histanocerus pubescens* Motschulsky

Body (Fig. 26) lightly pigmented, except for pronotal club, barbed processes on thoracic and abdominal terga, elytral apices, urogomphi, and major setae, all of which are yellowish-brown to dark brown in color. Vestiture consisting of major setae, all of which are darkly pigmented and borne on raised, conical processes, and scattered, shorter or lightly pigmented setae. Head with 4 paramedian pairs of major setae, 1 on each side of vertex, 2 in front of eye, and 1 on each eye. Pronotum bearing on its anterior edge a complex, club-like process (Fig. 27) consisting of a number of pigmented barbs and setae; center of disc with 3 pairs of pigmented, posteriorly-curved, barbed processes, each bearing a seta near the base, 7 discal and 11 marginal major setae on each side of barbed processes. Meso- and metaterga each with a pair of paramedian, barbed processes, and 2 major setae on each side of these. Abdominal terga 1 to 7 each with a pair of barbed processes each bearing a seta which is close to

the apex, 2 major setae on each side, and a lateral seta, which is particularly long and borne on a well-developed process. Abdominal tergum 8 without barbed processes, with 3 major setae on each side (including lateral seta). Ninth tergum with a pair of fine, simple, darkly-pigmented, widely separated urogomphi, and 4 major setae below the urogomphi on each side. Sterna each with a paramedian pair of lightly pigmented, long, fine setae. Elytral pads each with several major setae and a barbed process at the apex.

Material examined. Three pupae collected with a series of larvae and teneral adults in fruiting bodies of *Ganoderma* sp. in the Krau Game Reserve, Temerloh District, Pahang, MALAYSIA, Aug. 29, 1974, Lot 3721 J. F. Lawrence (J. Fleagle, collector) [MCZC].

FAMILY CHARACTERIZATION

Family PTEROGENIIDAE

Pterogeniidae Crowson 1955: 124.

With the general characters of Polyphaga: Cucujoidea.

Adult. Form oval to oblong, convex; length 1.5-3.5mm. Head globular, without neck, inclined and partly concealed by pronotum, without stridulatory files on occiput. Eye relatively small, coarsely facetted, oval to deeply emarginate, always bordered posteriorly by lateral outgrowth of head, occasionally (males of *Pterogenius*) greatly distorted by lateral expansion of frons. Frontal region flat or slightly concave, in *Histanocerus* with lateral collosities, in *Pterogenius* produced and elevated at apex and expanded laterally in male; frontoclypeal suture distinct; antennal insertions exposed (*Histanocerus*) or concealed (*Pterogenius*). Clypeus small, oval, lying in median emargination of frons and about 0.2 × its width, in male densely punctate and pubescent (*Histanocerus*) or impunctate and bearing pubescent fovea (*Pterogenius*, Figs. 28-29). Antennae 11-segmented, with very weak (*Pterogenius*) or strong (*Histanocerus*) 3- to 6-segmented, gradual club (Figs. 28-31); first antennal segment at least twice as long as second, in *Histanocerus* longer and asymmetrical, bearing apical process which may be curved or hooked (Figs. 15, 30-31). Mouthparts small relative to size of head, mouth cavity being less than half as wide as head behind eyes. Labrum semicircular, joined to clypeus by visible membrane. Mandibles wedge-like, with broad base, two apical teeth, membranous, hairy prostheca, similar basal lobe, extensive mola consisting of fine, transverse ridges, and slightly concave outer surface, bearing numerous hairs. Maxilla with 2-segmented, brush-like galea and articulated lacinia without apical hook; palp 4-segmented, the apical segment securiform. Labium with well-developed, broad ligula and 3-segmented palp. Gula strongly narrowed anteriorly.

Prothorax (Fig. 12) strongly transverse, lateral margins distinct with edges finely crenulate, base weakly bisinuate, not margined, anterior edge truncate. Prosternum short, strongly tumid, intercoxal process moderately broad, slightly expanded behind coxae, narrowly rounded and depressed at apex, fitting into depression on mesosternum. Procoxae slightly transverse, without internalized, lateral extensions, trochantin concealed, very small, and fused to coxal cowling; procoxal cavities closed internally, open externally. Scutellum transverse. Elytra not striate, with confused punctation and weak humeral calli, lateral edge of each with reflexed margin and broad epipleuron which extends to apex. Hindwing (Crowson 1955: fig. 159) with Media reduced and with 4 veins in the "anal" group, the first of which bisects the subcubital fleck. Mesosternum (Fig. 13) slightly convex, about as long as wide, with shallow, smooth, triangular depression at anterior edge; intercoxal process notched at apex, extending posteriorly beyond middle of coxae, which are globular and distinctly separated; coxal cavities not closed outwardly by sterna (mesepimera reaching cavities); trochantin exposed. Metasternum (Fig. 13) transverse, convex, flat in middle; median suture distinct, about 0.67 × as long as sternum; a pair of transverse ridges just in front of hind coxae, which are strongly transverse and narrowly separated. Metendosternite (Crowson 1944: fig. 76) with narrow stalk, reduced lamina, and anterior tendons located beyond middle of narrow arms. Tarsomeres 5-5-4 in both sexes, simple, subequal, except for last, which is as long as others taken together; claws simple, empodium well-developed, bearing 2 long setae. Trochanters weakly heteromeroid. Apices of all tibiae with 2 inner spurs and several spines; outer apical angle of protibia in *Histanocerus* (Fig. 14) expanded and bearing several stout spines.

Abdomen with 5 visible sternites, the first two (segments 3 and 4) connate, the first without lines or ridges. Sternite 7 unmodified, 8th sternite with short, median, basal strut, 9th segment with membranous apex, lateral struts joined for a short distance at base. Aedeagus (Figs. 10-11) of the inverted heteromeroid type, with elongate, ventral, basal piece, tegmen deeply divided forming two widely separated parameres converging at apices, and long, narrow, median lobe, with complex apical region. Ovipositor (Fig. 9) elongate, paraprocts and proctiger with supporting rods, coxite 3-segmented, terminal segment elongate, its apical portion narrow, extending well beyond vulva, more heavily sclerotized than base, almost glabrous except at apex; stylus terminal, elongate, heavily sclerotized. Spermatheca simple (*Histanocerus*) or convoluted (*Pterogenius*), its apex inclosed by a dome-like structure.

Pupa. See description on p. 29.
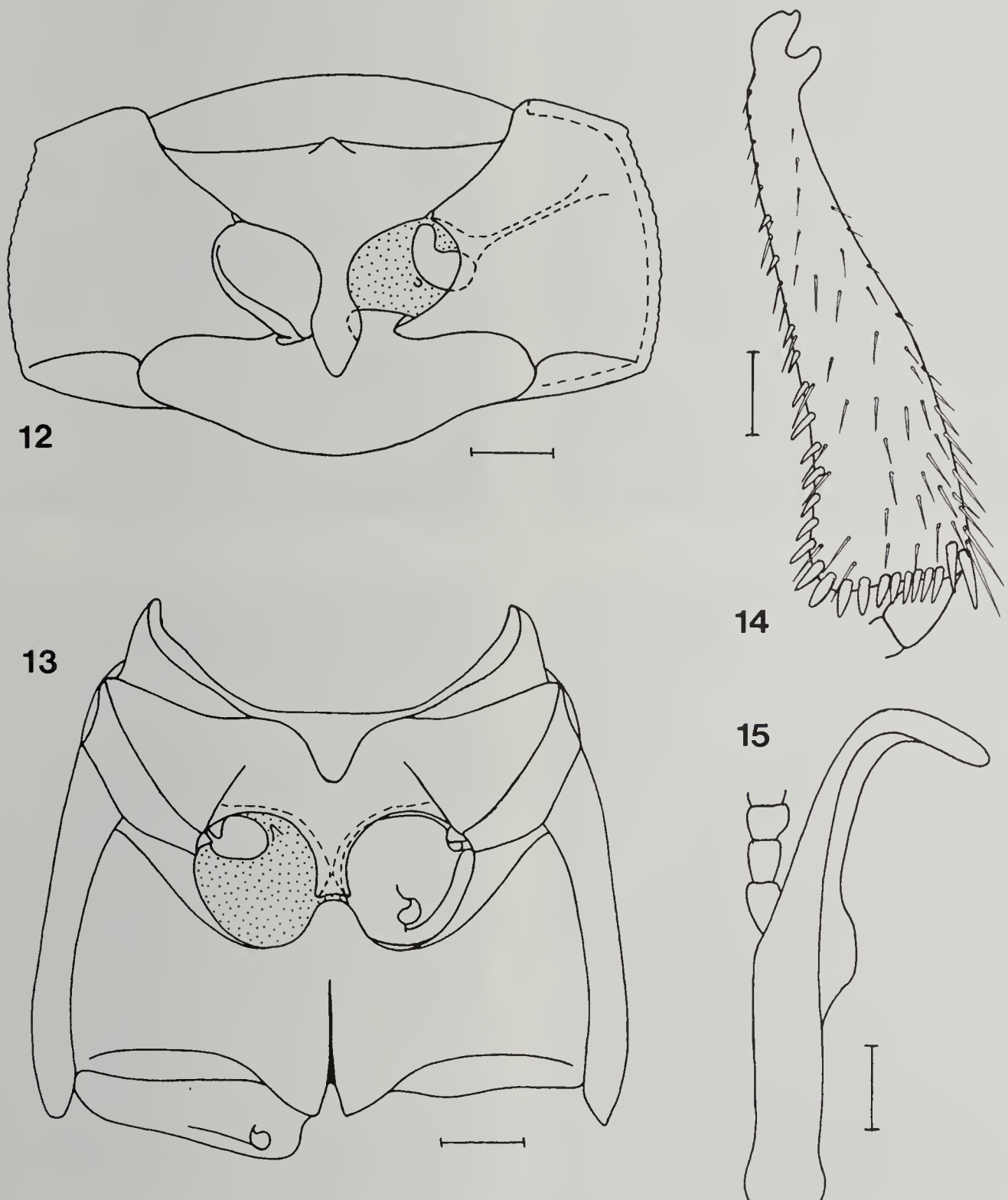
Figs. 12-13. *Pterogenius nietneri.* Adult male. 12) Prothorax, ventral view, left procoxa removed. 13) Pterothorax, ventral, right mesocoxa and left metacoxa removed. Fig. 14. *Histanocerus pubescens.* Adult male, left protibia, posterior. Fig. 15. *H. fleaglei.* Adult male, left antenna, segments 1-4, dorsal. (1 line = 0.125mm. for 12, 13, 15; 0.06mm. for 14).

Larva. (See figures for larval descriptions). Body elongate and subcylindrical, lightly sclerotized except for head and abdominal apex. Head exserted, obliquely prognathous, subglobular, with epicranial stem bent to left and lyriform frontal arms connected anteriorly by transverse ecdysial line; endocarina and ventral epicranial ridges absent. Ocelli 4 or 5 on each side. Antennal insertions partly concealed by antennal ridges, separated from mouth cavity by narrow bar. Antenna, short, 3-segmented, with long sensory appendix on segment 2 and very long terminal seta. Gula well-developed and elongate, separated from submentum by suture; gular sutures distinct, converging anteriorly. Mandibles asymmetrical, large, and wedge-shaped, with triangular base and 2 apical teeth; left mandible with scalloped cutting edge, mola elongate, parallel to long axis, concave, with 2 distal teeth and several transverse ridges alternating with rows of deep pits; right mandible with truncate process on cutting edge, mola oblique and convex with similar surface; both mandibles with several rows of very fine, cuticular outgrowths on dorsal surface, and 2 stout setae on outer edge; prostheca and basal lobe absent. Maxilla free almost to base of mentum, with elongate-oval articulating area; mala obliquely truncate, armed at apex with spines and setae, an uncus at inner third, and 2 heavy subapical spines at inner angle; cardo undivided externally; palp 3-segmented. Labium with small submentum, elongate mentum, short, quadrate prementum, and well-developed ligula with 2 setae; palp 2-segmented. Hypopharynx with distinct mola-like sclerome, in front of which are 2 setal brushes. Prothorax slightly larger than meso- or metathorax; coxae large and conical, fairly close together; spiracle annular-biforous, with accessory chambers dorsal. Legs well-developed, about equal in size; tarsungulus with 2 setae. Abdominal spiracles annular-biforous, with accessory chambers posterodorsal at angle of 45°, those on 8th segment enlarged. Ninth tergum with pair of urogomphi, simple or bifurcate; 8th and 9th sterna reduced and transverse; 10th segment reduced, transverse but somewhat pygopod-like, with several anal papillae.

Adult pterogeniids are similar in general form to certain cryptophagids (*Antherophagus*) and languriids (*Cryptophilus, Setariola*) as well as to a number of heteromerous groups, such as Byturidae, Biphyllidae, Mycetophagidae, Tetratomidae, Ciidae, and Tenebrionidae. The securiform maxillary palps, reduced clypeus, internally closed and externally open procoxal cavities, laterally "open" mesocoxal cavities, connate 3rd and 4th abdominal segments, and inverted heteromeroid aedeagus, in combination, will distinguish them from any of the above. Distinguishing characters of the larva have been given on p. 29.

The structure of the aedeagus in *Pterogenius* and *Histanocerus* is quite similar, and differences among the species of each are minor ones. Genital characters have not been used in the descriptions or keys presented below.

SYSTEMATIC REVIEW

Key to the genera of Pterogeniidae

1.   *Adult.* Antennal insertions more or less exposed; first antennal segment with apical process extending beyond articulation of segment 2 (Figs. 15, 30); antennal club distinct, its segments always transverse (Figs. 30, 31); outer apical angle of protibia expanded and bearing several stout spines (Fig. 14); head of male not laterally expanded, clypeus without pubescent fovea. *Larva.* Urogomphi simple and approximate (Figs. 4-5); sensory appendix of antenna distinctly longer than segment 3; abdominal tergum 8 unpigmented. Southeast Asia, East Indies .... *Histanocerus* Motschulsky

1'.   *Adult.* Antennal insertions completely concealed from above; first antennal segment without apical process; antennal club weak, its segments not transverse; outer apical angle of protibia not expanded; head of male laterally expanded, clypeus with pubescent fovea (Figs. 28-29). *Larva.* Urogomphi bifurcate (Fig. 3); sensory appendix of antenna subequal to segment 3 (Fig. 7); abdominal tergum 8 pigmented. Ceylon........
.... *Pterogenius* Candeze
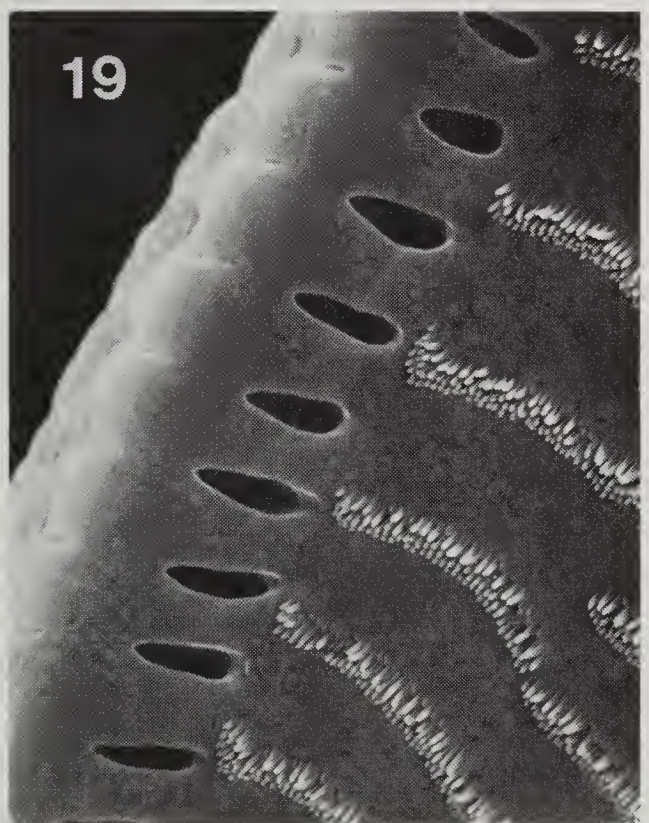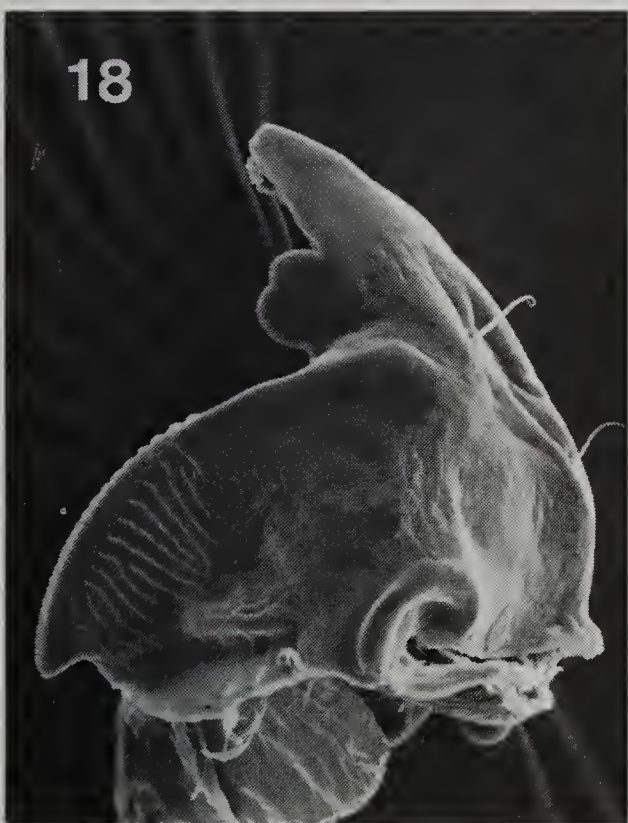
Figs. 16-19. *Pterogenius nietneri.* Larval mandibles. 16) Right mandible, ventral, 331x. 17) Left mandible, ventral, 324x. 18) Right mandible, dorsal, 350x. 19) Right mandible, section of dorsal surface adjacent to mola, 2800x.

Pterogenius Candeze

Pterogenius Candeze 1861: 363. Type species, by monotypy, *P. nietneri* Candeze.
Apogenia Pascoe 1866: 486. Unnecessary replacement name.

Members of this genus are easily distinguished by the characters given in
the key. The expansion of the head in the male is particularly striking, and
in the larger males of *P. nietneri* the head may exceed the prothorax in
width. Although anteriorly directed horns on the head and pronotum are
common in males of various Coleoptera (Ciidae, Tenebrionidae, Scarabaei-
dae), lateral expansion of the head is a relatively rare phenomenon. Nota-
ble examples occur in the Cerambycidae (*Tapeina transversifrons* Thom-
son), Erotylidae (*Zythonia fulva* Westwood), and Aglycyderidae (*Aglycy-
deres* spp.). This feature may be associated with male combat, but the acute
and slightly elevated edge of the entire frontal region suggests the possi-
bility of its use in the cooperative construction of egg galleries. The fovea
on the clypeus is also an uncommon secondary sexual character in beetles,
although foveae on the frons or vertex occur in males of several Ciidae.
These structures appear to be secretory and may be associated with the
production of a sex pheromone.

The two described species of *Pterogenius* are apparently restricted to the
island of Ceylon (Sri Lanka).

Key to adults of described species of *Pterogenius*

1. Antennal segment 3 more than 1.3 × as long as segment 2, not
curved in male; head of male greatly expanded, often broader
than pronotum, bearing a pubescent fovea which is more than
0.25 × as wide as clypeus (Fig. 28); pronotal punctation very
dense, the punctures confluent; size larger (usually 3mm. or
more) .... *P. nietneri* Candeze

1'. Antennal segment 3 less than 1.2 × as long as segment 2,
strongly curved in male (Fig. 29); head of male not as greatly
expanded, bearing a pubescent fovea which is less than 0.25 ×
as wide as clypeus (Fig. 29); pronotal punctation not as dense,
the punctures usually not confluent; size smaller (usually
less than 3mm.) .... *P. besucheti* Lawrence, n. sp.

Pterogenius besucheti Lawrence, **new species**

Individuals of this species are usually smaller than those of *P. nietneri*,
and the pronotal punctures are less dense and not confluent; males are
easily distinguished by the modifications of the third antennal segment.

Description. Length 2.3-3.0mm. Color dark reddish-brown to brownish-black,
head and prothorax usually darker than elytra. Vestiture of long, fine, densely
packed, inclined hairs. Head (Fig. 29) moderately to strongly expanded at sides,
almost as wide as prothorax in larger males; front edge strongly arcuate in female,
weakly so in male; clypeal fovea in male about 0.15 × as wide as base of clypeus,
and located near apical edge. Antenna of male about 1.2 × as long as pronotal
width, segment 1 twice as long as 2, segment 3 slightly longer than 2, strongly curved
and narrowed at base, with glabrous upper surface; segments 4-6 slightly longer
than wide, 7-11 forming a weak club; female antenna about as long as pronotal
width, segment 1 about 1.6 × as long as 2, segment 3 unmodified. Pronotum about
.6 × as long as wide, widest at middle, sides weakly rounded, with distinct, slightly
raised margins, visible for their entire lengths from above, and irregularly crenulate
edges; anterior angles almost right, posterior angles obtuse; disc moderately convex,
punctation coarse and dense, but not confluent. Elytra about 1.25 × as long as
wide and 2.3 × as long as pronotum, lateral margins narrow, not visible from above,
except at anterior end; disc moderately convex, steeply sloping laterally, grad-
ually so posteriorly; punctation somewhat finer than that of pronotum.

Types. Holotype, male, and allotype, female, CEYLON: Kandy, 600m., Jan. 15, 1970, Lot 3a, polypore on old tree stump (C. Besuchet and I. Löbl) [MHNG]. Paratypes: CEYLON: 13, same data as holotype [MHNG, MCZC]; 1, Ratnapura, Sabaragamuwa, Jan. 21, 1970, Lot 16b, sifted from dead leaves (C. Besuchet and I. Löbl) [MHNG].
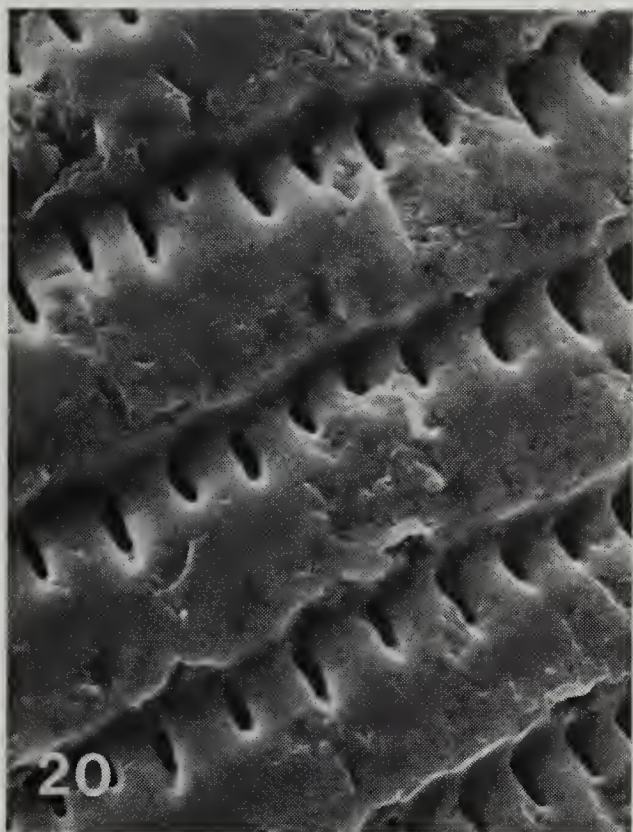

Fig. 20. *Pterogenius nietneri.* Right larval mandible, section of molar surface, 5240x. Figs. 21-23. *Histanocerus pubescens.* Larval mandibles. 21) Left mandible, mesal, 400x. 22) Right mandible, dorsal, 400x. 23) Right mandible, section of dorsal surface and adjacent mola, 4000x.

Pterogenius nietneri Candeze
(Fig. 28)

Pterogenius nietneri Candeze 1861: 364, pl. 3, fig. 8c. Type locality: Ceylon. Type not examined.

Males of this species differ from those of *P. besucheti* in having a more greatly expanded head and larger clypeal fovea and in lacking modifications on the third antennal segment (Fig. 28); both sexes may be distinguished by the very dense and confluent pronotal punctation.

Distribution. Known only from Ceylon.

Host Fungi. Dark polypore (possibly *Ganoderma* sp.). Stomach contents of a larva from Kanda-ela Reservoir consisted of large masses of brownish skeletal and binding hyphae cut into relatively small segments; no spores were seen.

Material Examined. CEYLON: 170, Hagkala, 1700-1800m., Jan. 28, 1970 (Besuchet & Löbl) [MHNG, MCZC]; 10, Kanda-ela Reservoir, 5.6 mi. SW Nuwara Eliya, 6200 ft., Feb. 10-21, 1970 (Davis & Rowe) [USNM]; 7, Peradeniya, 550m., Jan. 19, 1970 (Besuchet & Löbl) [MHNG]; 15, same locality, 1910 (Petch) [MCZC]; 1, Pidurutalagala, 2200m., Jan. 29, 1970 (Besuchet & Löbl) [MHNG].

Histanocerus Motschulsky

Histanocerus Motschulsky 1858: 112, fig. 16. Type species, by monotypy, *H. pubescens* Motschulsky.

Labidocera Gebien 1925: 117. Type species, by monotypy, *L. abnormis* Gebien.

Males and females of *Histanocerus* species are distinguished from those of *Pterogenius* by the enlarged first antennal segment, transverse antennal club segments, and expanded protibial apex. In general form they resemble members of the tenebrionid genus *Pentaphyllus*, which often occur in the same habitats, but *Pentaphyllus* have the eyes large and more coarsely facetted, the procoxal cavities closed behind, the first 3 visible abdominal sternites fused, and the first antennal segment unmodified. The asymmetrically lengthened first antennal segment of *Histanocerus* males is a relatively uncommon secondary sexual character, although it does occur in a number of laemophloeine Cucujidae. The structure may be involved in courtship, but it is also possible that it is used in male combat, as are the head and pronotal horns in other small fungus beetles (Tenebrionidae, Ciidae). Another peculiar feature occurring only in the *H. pubescens* section of the genus is the cavity formed between the reflexed anterolateral margin of the elytra and the humeral callus; this cavity is glabrous and shiny, in contrast to the surrounding area, and in several Malaysian specimens the cavity was occupied by one or two mites in the hypopial stage.

Specimens of *Histanocerus* have been seen from Malaysia, Java, Sumatra, Mindanao, and the Solomon Islands. A unique female from Shortland Island and some additional specimens from Mindanao were not described because of lack of adequate material. It is quite possible that the genus is more widespread in Southeast Asia and may also occur in New Guinea.

Both adults and larvae of *Histanocerus* occur in and feed upon the hyphal tissue of woody polypores, such as *Ganoderma* and *Trametes*. They are usually accompanied by bolitophagine and pentaphylline Tenebrionidae (*Bolitonaeus*, *Pentaphyllus*, etc.) and various species of Ciidae.

Key to adults of the described species of *Histanocerus*

(excluding *H. drescheri* (Pic); *see* p. 38)

1.   Each elytron with an impunctate, anterolateral cavity be-
      tween the humerus and epipleural carina; body more elongate
      (Fig. 31), TL/EW more than 1.7..2
1′.   Elytra without cavities; body shorter and broader (Fig. 30),
      TL/EW less than 1.7..4

2(1). Antennal club 3-segmented; body smaller and more elon-
       gate, length less than 1.8mm. and TL/EW more than 2.0.........
       .... *H. minutus* Lawrence, n. sp.
2′.   Antennal club with more than 4 segments; length more than
       2mm. or TL/EW less than 1.95..3

3(2″). Antennal club 6-segmented; length usually more than
       2.4mm.; punctation and pubescence denser; TL/EW usually
       more than 1.9; Philippines......................... *H. werneri* Lawrence, n. sp.
3′.   Antennal club 5-segmented; length usually less than 2.4mm.;
       punctation and pubescence sparser; TL/EW usually less than
       1.9 ....*H. pubescens* Motschulsky

4(2′). Prothoracic hypomeron punctate throughout; pronotal disc
       weakly arched anteriorly; elytral vestiture distinctly dual,
       with dense, decumbent hairs and sparser, erect ones; first an-
       tennal segment in the largest males only slightly hooked at
       apex (Fig. 30) .... *H. abnormis* (Gebien)
4′.   Prothoracic hypomeron with an impunctate and strigose area
       in its center; pronotal disc strongly arched anteriorly; ely-
       tral vestiture more uniform, all hairs more or less suberect
       and differing only slightly in angle of inclination; first an-
       tennal segment in largest males distinctly hooked at apex
       (Fig. 15) .... *H. fleaglei* Lawrence, n. sp.

Histanocerus abnormis (Gebien), **new combination**

(Fig. 31)

Labidocera abnormis Gebien 1925: 119, pl. 1, fig. 4. Type locality: Si-Oban I.,
    Mentawei Group, SUMATRA. Cotype, female, examined [MGFT].

    This species differs from *H. pubescens, H. werneri,* and *H. minutus* by
the short, broad body and the absence of a subhumeral, elytral cavity.
From *H. fleaglei* it is distinguished by the weakly arched pronotum, less
distinctly dual vestiture, and less strongly hooked apex on the first anten-
nal segment in the male. Specimens from Java and Sumatra differ slightly
from Malaysian individuals, being somewhat larger and more robust.

    Distribution. Sumatra, Java, Malaysia. Specimens examined from Men-
tawei, Sumatra [MGFT]; Fort de Kock, Sumatra [MGFT, USNM]; and
Krau Game Reserve, Temerloh District, Pahang, Malaysia [MCZC]. Gebien
cotype (not examined) from Tjompea, Java.

    Host Fungi. Trametes scabrosa (series with larvae); *Ganoderma* sp.
(1 specimen).

Histanocerus drescheri (Pic), **new combination**

Labidocera drescheri Pic 1937:304. Type locality: Goenoeng Tangkoeban Prahoe, JAVA. Types in Museum National d'Histoire Naturelle, Paris (not examined).

This species was not included in the key, since the types were not available for study. According to Pic's description, the species is larger than most *Histanocerus* (2.5—3.5 mm.), and differs from *H. abnormis* in being less robust with the thorax less transverse. The species is most similar to *H. pubescens* and *H. werneri* in general body form.
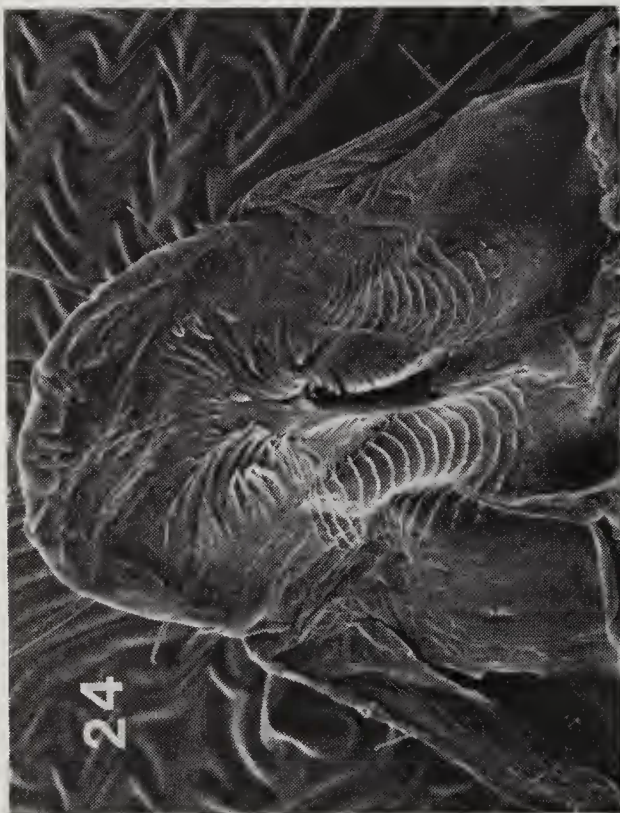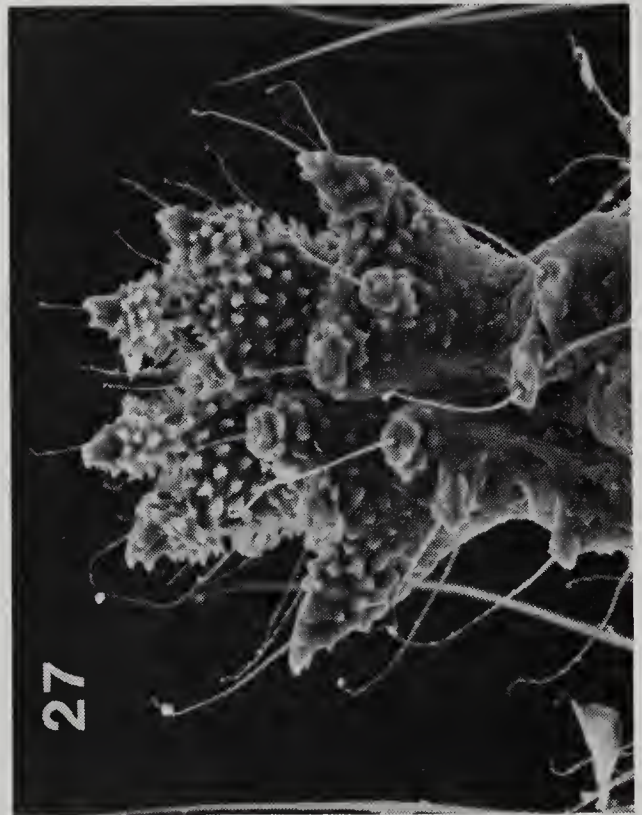
Figs. 24-25. *Pterogenius nietneri*. Larva. 24) Epipharynx and pharynx, ventral, 340x. 25) Apex of right mala, anteromesal, 587x. Figs. 26-27. *Histanocerus pubescens*. 26) Pupa, dorsal, 39x. 27) Pupal thoracic club, 403x.

Histanocerus fleaglei Lawrence, **new species**

This species is distinguished from members of the *H. pubescens* group by the absence of a subhumeral elytral cavity, gradually expanded epipleura, and shorter and broader body form. From *H. abnormis* it differs in having a smooth, shiny area on the hypomeron, larger pronotal punctures, a more strongly arched pronotum in the male, and a more distinctly hooked apex on the first segment of the male antenna.

Fig. 28. *Pterogenius nietneri.* Adult male. Fig. 29. *P. besucheti.* Adult male, head and pronotal apex. Fig. 30. *Histanocerus abnormis.* Adult male. Fig. 31. *H. werneri,* adult male.

Description. Length 1.85–2.40 mm. Color yellowish brown to dark reddish-brown, head and prothorax usually darker than elytra. Vestiture of long, fine, moderately dense, subdecumbent yellowish hairs, mixed with sparsely scattered suberect hairs in rows on elytra. Head strongly declined, flat in female, in male vertex concave and frontoclypeal region with strongly raised callosities over antennal insertions. Antenna of male with segment 1 strongly curved and hooked at apex, the tip narrowly rounded, not notched (Fig. 15); antennal club 5-segmented. Pronotum about 0.53 × as long as wide, widest at basal fourth, sides gradually converging towards apex, with narrow, slightly raised margins, not entirely visible from above, and smooth edges; disc strongly convex, in male steeply sloping anteriorly; punctation moderately coarse and dense, punctures distinctly larger than eye facets and separated by 0.5 to 1 diameter. Elytra about 1.14 × as long as wide and 2.19 × as long as pronotum, widest near anterior edge, sides gradually converging posteriorly; lateral margins narrow and finely serrate; disc moderately convex, subhumeral cavities absent; punctation about the same as on pronotum. Hypomeron with a smooth, shiny area in center, just laterad of coxa. Protibia strongly expanded at apex, outer angle with several short spines. Metasternum 0.30 × as long as wide. Elytral epipleura gradually expanded at anterior end.

Types. Holotype, male, and allotype, female, MALAYSIA: Selangor: Lima Blas Estates, Jan. 15, 1975, Lot 3745 J. F. Lawrence (J. Fleagle, coll.), ex *Amauroderma rugosum* (Blume and Nees) Doidge [MCZ No. 32292]. Paratypes: MALAYSIA: Selangor: 14, same data as holotype [FMNH, MCZC, USNM]; 3, same locality, date, collector, Lot 3748 J. F. Lawrence, ex *Ganoderma* sp. [MCZC].

Histanocerus minutus Lawrence, **new species**

Individuals of this species resemble those of *H. werneri* in general body form, punctation, and pubescence, but are easily recognized by the small size and 3-segmented antennal club.

Description. Length 1.75 mm. Color of head and prothorax reddish-brown, elytra dark yellowish-brown. Vestiture of long, fine, dense, subdecumbent, yellowish hairs. Head moderately declined, vertex flat, frontoclypeal region in male with weak callosities over antennal insertions. Antenna of male with segment 1 slightly curved and subacute at apex; antennal club 3-segmented. Pronotum 0.62 × as long as wide, widest at middle, sides weakly rounded, with narrow, slightly raised margins, visible for their entire lengths from above, and crenulate edges; disc slightly convex, barely sloping anteriorly; punctation fine and dense, punctures about as large as eye facets and separated by half a diameter or less. Elytra 1.37 × as long as wide and 2.20 × as long as pronotum, widest near middle, sides subparallel for anterior two-thirds, gradually converging and broadly rounded at apices; lateral margins very narrow; disc moderately convex, subhumeral cavities present. Hypomeron granulate and strigose. Protibia weakly expanded at apex, outer angle with several long spines. Metasternum 0.45 × as long as wide. Elytral epipleura abruptly expanded at anterior end.

Types. Holotype, male, and allotype, female, MALAYSIA: Pahang: Krau Game Reserve, Temerloh District, Aug. 29, 1974, Lot 3721 J. F. Lawrence (J. Fleagle, coll.), ex *Ganoderma* sp. [MCZ No. 32293]. Paratype: MALAYSIA: same data as holotype [MCZC].

Histanocerus pubescens Motschulsky

Histanocerus pubescens Motschulsky 1858: 112, fig. 16. Type locality: "Ind. or." Lectotype, male, and 9 paralectotypes examined [ZMMU].

This species is distinguished from *H. abnormis* and *H. fleaglei* by the presence of a subhumeral elytral cavity and from *H. minutus* and *H. werneri* by the less elongate body form and 5-segmented antennal club. The type series differs from Malaysian specimens only in size, the length being 2.00–2.40 mm. in the former and 1.85–2.05 mm. in the latter. Other details, including the male genitalia, do not differ significantly. In addition to a series from the Temerloh District, Pahang and the Kuala Kangsar

District, Perak [MCZC], 4 specimens from Barungkot, Upi, Cotabato Province, Mindanao [FMNH] may also belong to this species, their size range even closer to that of the type series. It is unfortunate that Motschulsky's type locality is so vague.

Distribution. Malaysia and East Indies; Philippines?

Host Fungi. Ganoderma sp.

Histanocerus werneri Lawrence, new species

(Fig. 31)

This species differs from members of the *H. abnormis* group by the presence of a subhumeral elytral cavity, abruptly expanded epipleura, and more elongate body form. It is distinguished from *H. pubescens* by the denser punctation and vestiture and more elongate form, from *H. minutus* by the larger size, and from both by the 6-segmented antennal club.

Description. Length 2.35–2.55 mm. Color yellowish-brown to dark reddish-brown, head and prothorax usually darker than elytra. Vestiture of long, fine, dense, subdecumbent, yellowish hairs. Head weakly declined, vertex flat, frontoclypeal region in male with strong callosities over antennal insertions. Antenna of male with segment 1 weakly curved apically, not angulate or hooked, notched at tip; antennal club 6-segmented. Pronotum about 0.59 × as long as wide, widest at middle, sides weakly rounded, with narrow, slightly raised margins, visible for their entire lengths from above, and crenulate edges; disc slightly convex, barely sloping anteriorly; punctation fine and dense, punctures about as large as eye facets and separated by less than 1 diameter. Elytra about 1.38 × as long as wide and 1.95 × as long as pronotum, widest near middle, sides subparallel for anterior two-thirds, gradually converging and broadly rounded at apices; lateral margins very narrow; disc moderately convex, subhumeral cavities present. Hypomeron granulate and strigose. Protibia weakly expanded at apex, outer angle with several long spines. Metasternum 0.45 × as long as wide. Elytral epipleura abruptly expanded at anterior end.

Types. Holotype, male, and allotype, female, PHILIPPINES: Mindanao: E. slope Mt. McKinley, 5200 ft., Davao Prov., Aug. 20, 1946, rotten woody polypore (F. G. Werner, coll.) [FMNH]. Paratypes: PHILIPPINES: Mindanao: 6, same data as holotype [FMNH, MCZC]; 2, same locality, 6500 ft., Sept. 3, 1946, Lot 43, dead polypore (F. G. Werner, coll.) [FMNH]; 3, Meran, E. slope Mt. Apo, 6000 ft., Davao Prov., Nov. 5-9, 1946, Lot 131, decayed woody polypores (F. G. Werner, coll.) [FMNH].

MORPHOLOGICAL AND EVOLUTIONARY CONSIDERATIONS

A discussion of the phylogenetic relationships of the family Pterogeniidae or any other heteromeran family is hardly possible until the phylogeny of the entire section is examined, and the latter, in turn, is dependent upon a detailed analysis of the morphological features on which this phylogeny is based. Many characters used in heteromeran classification have been vaguely defined and their use by different authors has not been consistent. Although Crowson (1955; 1960; 1966) and more recently Doyen (1972), Watt (1967; 1974a; 1974b), and others have begun to introduce new characters and to more carefully analyze the old ones, much more work of this sort is still needed.

It is beyond the scope of the present paper to provide the complete analysis called for above, but perhaps it will suffice for me to discuss briefly several of the adult and larval features commonly used in Heteromera classification, to give an account of their distribution, within and

among the heteromeran taxa I have been able to study, and to then compare these to the condition found in the Pterogeniidae. Included will be some new features which have been discovered through the use of the scanning electron microscope, and some functional considerations of these and other more traditional characters used in studies of heteromeran relationships.

List of Taxa

The following annotated list of 58 higher taxa of Heteromera will be referred to in the discussion by means of the abbreviations in square brackets. Although the classification follows that of Crowson (1955; 1966; 1967) and Watt (1967; 1974a; 1974b) for the most part, a number of subfamilial groups are treated separately where family limits are uncertain and intra-familial variation too great. Any changes in family limits or excluded genera of uncertain affinities are also indicated below. A few groups are left out altogether, especially where larvae are not known. Most genera examined are listed; those with an asterisk are unknown to me as larvae (except for descriptions from the literature), while those with a double asterisk have not been described (or very poorly so) as larvae.

1. Byturidae [BYTU]. *Byturus, Byturellus.*
2. Biphyllidae [BIPH]. *Biphyllus, Anchorius, Goniocoelus.*
3. Mycetophagidae: Mycetophaginae [MYCP]. *Mycetophagus, Litargus, Typhaea.*
4. Mycetophagidae: Bergininae [BERG]. *Berginus.***
5. Tetratomidae: Piseninae [PISN]. *Pisenus.*
6. Tetratomidae: Tetratominae [TETR]. *Tetratoma, Incolia, Eupisenus.*
   The last genus is normally placed with *Pisenus,* but both larval and adult characters agree with the tetratomines.
7. Tetratomidae: Penthinae [PNTH]. *Penthe.*
8. Melandryidae: Hallomeninae [HALL]. *Hallomenus.* This is usually placed in the Eustrophinae but is isolated here because of its distinctive larva.
9. Melandryidae: Eustrophinae [EUST]. *Eustrophinus, Eustrophopsis.*
10. Melandryidae: Melandryinae [MLDR]. *Melandrya, Zilora, Orchesia,* etc.
11. Melandryidae: Osphyinae [OSPH]. *Osphya.**
12. Mordellidae [MORD]. *Tomoxia, Mordella.*
13. Pterogeniidae [PTER]. *Pterogenius, Histanocerus.*
14. Ciidae: Sphindociinae [SPHN]. *Sphindocis.*
15. Ciidae: Ciinae [CIIN]. *Cis, Xylographus,* etc.
16. Archeocrypticidae [ARCH]. *Enneboeus.* This family was described briefly by Watt (1974b), although the name was originally proposed by Kaszab (1964) on the basis of South American and Oriental forms thought to be tenebrionids. Also included is the North American "tenebrionid" genus *Uloporus* Casey (1889), which may be synonymous with *Enneboeus* Waterhouse. This group is currently being revised by J. C. Watt.
17. Monommidae [MONM]. *Hyporhagus.*
18. Colydiidae: Colydiinae [COLY]. *Aulonium, Namunaria,* etc. This is meant to include most of the tribes not included in the next subfamily. Excluded from consideration are *Myrmechixenus* and the orthocerine group.
19. Colydiidae: Bothriderinae [BOTH]. *Deretaphrus, Bothrideres.*
20. Zopheridae: Ulodinae [ULOD]. *Ulodes.*** Watt (1974b) has removed *Ulodes* and its relatives from the Tenebrionidae.
21. Zopheridae: Usechinae [USEC]. *Usechus.*

22. Zopheridae: Zopherinae [ZOPH]. *Zopherus, Nosoderma, Phellopsis.*
23. Perimylopidae [PERI]. *Hydromedion.* See Watt (1967).
24. Chalcodryidae [CHAL]. *Chalcodrya.** See Watt (1974a).
25. Tenebrionidae: Zolodininae [ZOLO]. *Zolodinus.**
26. Tenebrionidae: Diaperinae [DIAP]. *Diaperis, Eleates, Bolitotherus,* etc. This and the above subfamily are used in the sense of Watt (1974b).
27. Tenebrionidae: Tenebrioninae, etc. [TENB]. This includes the rest of Watt's subfamilies, which are generally consistent with respect to the characters discussed below.
28. Prostomidae [PRST]. *Prostomis* and *Dryocora.** Crowson (1967) added the genus *Paralindria* Olliff (= *Serrotibia* Reitter) and *Cheilopoma* Murray. On the basis of adults only, the former appears to be related to the Trogocryptinae (see below) and the latter may be a tenebrionid.
29. Cephaloidae: Nematoplinae [NEMA]. *Nematoplus.* Mamayev (1973) has recently described the larva from the U.S.S.R. and I have reared the Nearctic species.
30. Cephaloidae: Cephaloinae [CEPH]. *Cephaloon.*
31. Cephaloidae: Stenotrachelinae [STEN]. *Stenotrachelus.**
32. Oedemeridae: Calopodinae [CALO]. *Calopus.*
33. Oedemeridae: Oedemerinae, etc. [OEDM]. *Ditylus, Nacerda,* etc.
34. Pedilidae: Eurygeniinae [EURY]. *Pergetus.* This and the next subfamily are included in a broadly defined Anthicidae by Crowson (1955), but the larvae appear to be of a completely different type. I prefer to retain the old concept of Pedilidae for their inclusion.
35. Pedilidae: Pedilinae [PEDL]. *Pedilus.*
36. Synchroidae [SYNC]. *Synchroa, Mallodrya.* **
37. Mycteridae: Mycterinae & Lacconotinae [MYCT]. *Mycterus, Lacconotus,* etc.
38. Mycteridae: Hemipeplinae [HEMP]. *Hemipeplus.*
39. Boridae [BORI]. *Boros.*
40. Trictenotomidae [TRCT]. *Trictenotoma.**
41. Pythidae [PYTH]. *Pytho, Priognathus,* etc.
42. Pyrochroidae: Ischaliinae [ISCH]. *Ischalia.** This and the following are aberrant pyrochroids, which may be removed when immature stages are discovered.
43. Pyrochroidae: Lemodinae [LEMO]. *Lemodes.***
44. Pyrochroidae: Pyrochroinae [PYRO]. *Dendroides, Schizotus,* etc.
45. Othniidae: Othniinae [OTHN]. *Elacatis.*
46. Othniidae: Trogocryptinae [TROG]. *Trogocryptus,** Holosternus,** Anepsicus,** Cissocryptus,** Eurycratus,** Trogocryptoides,** Ocholissa,** Szekessya,** Serrotibia,** * and *Prostominia.* Crowson (1955) placed *Trogocryptus* and its allies, including *Prostominia,* in the Othniidae. Lawrence (1971a) suggested that *Szekessya* might be a prostomid, but further examination has revealed its affinities with the trogocryptines. The placement of this group within the Othniidae is still open to question, and it is possible that they are more closely related to Salpingidae.
47. Salpingidae: Aegialitinae [AEGI]. *Aegialites.* Spilman (1967) removed this genus from the Othniidae, where it was placed by Crowson (1955). Perhaps a better solution would be to unite the Othniidae, Salpingidae, and perhaps Inopeplidae into a family, but this would leave the problem of the transition between this complex and the Pythidae-Pyrochroidae.
48. Salpingidae: Salpinginae [SALP]. This includes the Japanese *Istrisia,* whose larva has some of the characteristics of both Pythidae and Othniidae.
49. Dacoderidae [DACO]. *Dacoderus,** Tretothorax.** These two genera were included in a separate family by Watt (1967), but they appear to be related to salpingids.
50. Inopeplidae [INOP]. *Inopeplus, Diagrypnodes.*
51. Scraptiidae: Anaspidinae [ANAS]. *Anaspis.* This and the next subfamily were considered as derivatives of the Melandryidae by Crowson (1966), but the

larvae appear to have much more in common with the anthicid group, as was indicated by Böving and Craighead (1931).

52. Scraptiidae: Scraptiinae [SCRP]. *Scraptia*,* *Canifa*.

53. Anthicidae: Macratriinae [MACR]. *Macratria*.** This is included in the Pedilidae in North American works (Arnett 1968), but the adult characters indicate a closer relationship to anthicids.

54. Anthicidae: Anthicinae [ANTH]. *Anthicus, Notoxus,* etc.

55. Anthicidae: Lagrioidinae [LAGD]. *Lagrioida*.** This group was proposed by Abdullah (1968), but the larva, which is apparently known to Crowson, has not been described.

56. Euglenidae [EUGL]. *Elonus*,** *Escalerosia*,* unassociated larvae (identified using Hayashi 1972).

57. Rhipiphoridae [RHIP]. *Trigonodera*,** *Rhipiphorus*,* etc.

58. Meloidae [MELO]. *Pyrota*,* *Nemognatha*,* etc. These last two families are highly specialized and not necessarily related. Rhipiphoridae are thought to have evolved from mordellids, and meloids have been associated with cephaloids (Crowson, 1955).

The following alphabetical list of abbreviations may aid the reader in referring back to the taxa discussed above: AEGI: 47. Salpingidae: Aegialitinae; ANAS: 51. Scraptiidae: Anaspidinae; ANTH: 54. Anthicidae: Anthicinae; ARCH: 16. Archeocrypticidae; BERG: 4. Mycetophagidae: Bergininae; BIPH: 2. Biphyllidae; BORI: 39. Boridae; BOTH: 19. Colydiidae: Bothriderinae; BYTU: 1. Byturidae; CALO: 32. Oedemeridae: Calopodinae; CEPH: 30. Cephaloidae: Cephaloinae; CHAL: 24. Chalcodryidae; CIIN: 15. Ciidae: Ciinae; COLY: 18. Colydiidae: Colydiinae: DACO: 49. Dacoderidae; DIAP: 26. Tenebrionidae: Diaperinae; EUGL: 56. Euglenidae; EURY: 34. Pedilidae: Eurygeniinae; EUST: 9. Melandryidae: Eustrophinae; HALL: 8. Melandryidae: Hallomeninae; HEMP: 38. Mycteridae: Hemipeplinae; INOP: 50. Inopeplidae; ISCH: 42. Pyrochroidae: Ischaliinae; LAGD: 55. Anthicidae: Lagrioidinae; LEMO: 43. Pyrochroidae: Lemodinae; MACR: 53. Anthicidae: Macratriinae; MELO: 58. Meloidae; MLDR: 10. Melandryidae: Melandryinae; MONM: 17 Monommidae; MORD: 12. Mordellidae; MYCT: 37. Mycteridae: Mycterinae and Lacconotinae; MYCP: 3. Mycetophagidae: Mycetophaginae; NEMA: 29. Cephaloidae: Nematoplinae; OEDM: 33. Oedemeridae: Oedemerinae etc.; OSPH: 11. Melandryidae: Osphyinae; OTHN: 45. Othniidae: Othniinae; PEDL: 35. Pedilidae: Pedilinae; PERI: 23. Perimylopidae; PISN: 5. Tetratomidae: Piseninae; PNTH: 7. Tetratomidae: Penthinae; PRST: 28. Prostomidae; PTER: 13. Pterogeniidae; PYRO: 44. Pyrochroidae: Pyrochroinae; PYTH: 41. Pythidae; RHIP: 57. Rhipiphoridae; SALP: 48. Salpingidae: Salpinginae; SCRP: 52. Scraptiidae: Scraptiinae; SPHN: 14. Ciidae: Sphindociinae; STEN: 31. Cephaloidae: Stenotrachelinae; SYNC: 36. Synchroidae; TETR: 6. Tetratomidae: Tetratominae; TENB: 27. Tenebrionidae: Tenebrioninae etc.; TRCT: 40. Trictenotomidae; TROG: 46. Othniidae: Trogocryptinae; ULOD: 20. Zopheridae: Ulodinae; USEC: 21. Zopheridae: Usechinae; ZOLO: 25. Tenebrionidae: Zolodininae; ZOPH: 22. Zopheridae: Zopherinae.

Adult Characters

Among adult characters used in heteromera classification, the frontoclypeal suture has a somewhat erratic distribution, and in some groups its occurrence is quite variable. Its presence appears to be primitive in the Heteromera, although it is lacking in Biphyllidae and Byturidae. Those taxa in which the frontoclypeal suture occurs include MYCP, BERG, PISN, TETR, PNTH, HALL, EUST, OSPH, PTER, SPHN, CIIN, ARCH, PERI, CHAL, DIAP, TENB, PRST, ISCH, LEMO, INOP, ANAS, SCRP, ANTH, LAGD, EUGL, and MELO. In chalcodryids and tenebrionids, however, the condition is variable, and the same is true for inopeplids and the scraptiid-anthicid group.

The concealment of the antennal insertions is another variable character in many Heteromera, and it may be associated with the degree of substrate locomotion practiced by the adult. The insertions are always concealed in SPHN, CIIN, ARCH, MONM, COLY, USEC, ZOPH, ZOLO, DIAP, TENB, and DACO. The condition in Pterogeniidae is variable, and the lack of antennal ridges in *Histanocerus* is probably connected with the need to move the enlarged first antennal segment. The degree of concealment also varies in BIPH, MYCP, SYNC, PYTH, and TROG. Slight concealment occurs in PISN and BORI.

The terminal segment of the maxillary palps in many Heteromera may be spindle-shaped or cylindrical, although usually truncate at the apex. In a number of taxa, and especially in those which are active on surfaces, the apex is distinctly enlarged and securiform or cultriform. This condition occurs in MLDR, OSPH, MORD, PTER, ARCH, CHAL, NEMA, CEPH, STEN, CALO, OEDM, EURY, PEDL, SYNC, MYCT, HEMP, TRCT, PYTH, ISCH, LEMO, PYRO, ANAS, SCRP, MACR, ANTH, LAGD, and EUGL. In some of these (NEMA, OEDM), the apical expansion is only slight.

The degree of development of the coxal cowling formed by the prosternal and pronotal projections has always been a major classificatory character in beetles, and it is usually expressed by the terms "open" and "closed" coxal cavities. Four conditions are possible (although they obviously grade into one another): internally and externally open cavities, those internally open and externally closed, those internally closed and externally open, and those internally and externally closed. The first condition (int. open/ext. open) always occurs in BERG, TETR, PNTH, OSPH, SPHN, MONM, USEC, ZOLO, CEPH, STEN, BORI, TRCT, ISCH, PYRO, EUGL, and MELO. In CIIN, the int. open/ext. open condition is predominant but not universal, in BOTH it occurs in some forms, in PEDL it occurs in all but some Australian ictistygnines (which have an external closure), in PYTH only the genus *Sphalma* has a narrow internal closure, and in SALP the int. open/ext. open condition occurs only in *Istrisia*. The second condition (int. open/ext. closed) is found in COLY, BOTH, ULOD, ZOPH, and PERI. The int. closed/ext. open condition is characteristic of MYCP, PISN, HALL, EUST, MLDR, MORD, PTER, NEMA, CALO, OEDM, EURY, SYNC, MYCT, HEMP, LEMO, TROG, AEGI, SALP, DACO, INOP, ANAS, SCRP, MACR, ANTH, LAGD, and RHIP, as well as *Sphalma*. Finally, the double closure (internal and external) occurs in BYTU, BIPH, ARCH, CHAL, DIAP, TENB, PRST, and OTHN. The primitive condition of the procoxal cavities is difficult to ascertain. Among those Languriidae which Sen Gupta and Crowson (1971) have proposed as possible ancestors of the Heteromera, the Xenoscelinae (=Loberinae) have the int. open/ext. open condition, with an external closure in one genus, the int. closed/ext. open condition occurs in Toraminae and Setariolinae, and a double closure occurs in the Cryptophilinae. Within the Heteromera, double closure occurs in biphyllids and byturids, but the int. open/ext. open and int. closed/ext. open conditions also occur in undoubtedly primitive forms.

Two other characters closely associated with the above are the form and extent of the prosternal intercoxal process, which separates the procoxae externally, and the portion of the procoxa which is concealed by

the lateral part of the coxal cowling. The intercoxal process may be broad to very narrow or laminate, or it may be reduced and not extend very far posteriorly between the coxae; the apex may be strongly expanded and joined to the postcoxal process of the hypomera, slightly expanded, truncate, or acute. Strongly expanded apices occur in ARCH, COLY, BOTH, ULOD, USEC, ZOPH, PERI, CHAL, OTHN, TROG, and AEGI, and are associated with externally closed or narrowly open cavities. Another distinctive condition is the extremely narrow and often shortened intercoxal process, which may be absent altogether in some forms. This occurs in surface-dwelling forms with conical, subcontiguous procoxae, such as EUST, MLDR, OSPH, MORD, NEMA, CEPH, STEN, CALO, OEDM, EURY, PEDL, MYCT, PYTH, ISCH, LEMO, PYRO, SALP, ANAS, SCRP, MACR, ANTH, EUGL, RHIP, and MELO.

The prothoracic pleurocoxal mechanism has been discussed in detail by Hlavac (1972; 1975). Heteromera, for the most part, have a specialized, reduced type of pleurocoxal mechanism, and in many cases the trochantin and much of the procoxa is enclosed by the coxal cowling. In an extreme case, the internalized portion of the procoxa is more than half as long as or even longer than the visible portion. This type occurs in MONM, COLY, BOTH, ULOD, USEC, ZOPH, ZOLO, DIAP, TENB, PRST, TROG, AEGI, SALP, DACO, and INOP. Other forms with more than a slight internalization of the procoxa include MLDR, PERI, CALO, OEDM, EURY, PEDL, SYNC, MYCT, HEMP, BORI, PYTH (*Sphalma*), EUGL, and LAGD. Most of the primitive Heteromera, including the pterogeniids, have no internalized portion at all.

The lateral closure of the mesocoxal cavities by the meso- and metathoracic sterna (closed cavities), as opposed to their closure by the mesepimera (open cavities), represents a dichotomy often used in heteromeran keys. The closure by the sterna is always associated with a hidden mesotrochantin, but in the eustrophine melandryids the trochantin is concealed although the mesocoxal cavities are "open." Open cavities are apparently primitive, and closure by the sterna has occurred a number of times in MYCP (*Typhaea*), BERG, MONM, COLY, BOTH, ULOD, USEC, ZOPH, some TENB, MYCT, HEMP, OTHN, TROG, AEGI, SALP, DACO, and INOP. The interlocking mechanism between the mesosternum and metasternum at the midline might be a useful new character in heteromeran classification, but I have not taken the time to analyze it properly. A number of forms, including the Pterogeniidae, have a process on one of the sterna which fits into a notch on the other, but some forms have double notches, while in others the two sterna appear to lack any interlocking structures.

The fusion of basal abdominal sternites is an extremely variable condition and one which is difficult to determine for various reasons. In some heavily sclerotized forms, the segments may be united by membranes which are concealed by cuticular abutments (*see* Watt 1967: 117). In lightly sclerotized forms, on the other hand, it may be difficult to distinguish connate segments from "free" ones (*see* Lawrence, 1971b: 4-5). Often, the first two visible sternites (3 and 4) are fused and immovable (although with a distinct suture), the joint between the second and third (4-5) is less flexible, and that between the posterior segments is completely flexible. Sternites 3 and 4 are definitely connate in PNTH, some MLDR,

PTER, SPHN, ARCH, PRST, STEN, CALO, SYNC, TRCT, some PYTH (*Sphalma*), ISCH, some TROG, AEGI, some SALP, LAGD, and EUGL, and in some of these (PNTH, CALO, TRCT, TROG) sternite 5 may be partially fused to 4. In *Elacatis* (OTHN) the basal sternites may be connate, but the entire abdomen is lightly sclerotized. Sternites 3 through 5 are connate in MONM, COLY, BOTH, ULOD, USEC, ZOPH, PERI, CHAL, ZOLO, DIAP, TENB, MYCT, HEMP, and BORI; in MONM, COLY, BOTH, USEC, and CHAL, sternite 6 may also be fused to 5. In DACO the sternites appear to be fused externally in dry specimens, but there is concealed membrane between each of the pairs of segments. In only two groups (AEGI and EUGL) is the suture between 3 and 4 lost entirely.

Wing venation in the Heteromera exhibits relatively little variation, the main characters involving the radial cell and Radial Sector, subcubital fleck, wedge cell, and number of veins between the Cubitus and jugal area (anal veins according to Crowson, but including the posterior branch of the Cubitus according to Ponomarenko 1973). The radial cell, wedge cell, and anal veins drop out readily in small forms, but the subcubital fleck remains in some of the smallest species, even in some Ciidae with reduced wings. An entire subcubital fleck occurs in MYCP, BERG, PISN, TETR, EUST, OSPH, SPHN, ARCH, COLY, ULOD, CHAL, ZOLO, some TENB, PRST, CALO, EURY, PEDL, SYNC, MYCT, BORI, PYTH, OTHN, TROG, SALP, MACR, LAGD, and EUGL. In a few taxa (BYTU, PTER, and LEMO) the fleck is divided by the posterior branch of the Cubitus, while in CIIN, which lack this vein, the fleck is very close to the main branch of the Cubitus and is also divided into two parts by what may be a remnant of the posterior branch.

The metendosternite does not appear to be particularly useful in determining heteromeran relationships. The stalk is usually relatively long, the laminae moderately well-developed, and the anterior tendons out on the arms. Pterogeniidae have the stalk narrow and the laminae very reduced, as do *Sphindocis* and the tenebrionid group. Female genitalia have been studied by Watt (1974a; 1974b) for certain heteromeran groups, but I have insufficient comparative data at present to pursue this character complex.

The male genitalia have been examined for all of the taxa listed above, but a proper analysis of these structures is beyond the scope of this paper. Among the forms studied there is a great deal of variation, and homologies are often difficult to ascertain. According to Crowson (1955: 114), the heteromeran aedeagus evolved from a primitive cucujoid type (ring-shaped tegmen bearing a ventral, basally projecting process and dorsal, articulated, distally projecting parameres) by the loss of the ventral portion of the ring, leaving the entire tegmen dorsad of the median lobe. Within the Heteromera, the Biphyllidae and Byturidae have the most clavicorn-like aedeagus, in that the tegmen does encircle the median lobe and does bear a median, basoventral process; the parameres, however, are fused to the apex of the tegmen. The typical heteromeran aedeagus consists of a dorsal, trough-like tegmen, which may or may not be divided into an apical and basal portion, and a ventral median lobe, partially enclosed by the sides of the tegmen. In a number of groups, however, the tegmen is ventral to the median lobe; this is thought to be the result of a torsion of the external genitalia. Determining the position of the tegmen is often

difficult, since it must be examined while still within the abdomen and also while extruded; in some forms it appears to lie in a lateral position within the abdomen. The tegmen may consist of a single piece, or it may include a basal piece and one or two apical parameres. In addition, there may be lateral struts which partly encircle the median lobe or accessory processes, which are usually articulated and attached to the single paramere. In *Pisenus*, the basal piece is sclerotized ventrally, but at its apex, it extends dorsally and bears a pair of articulated parameres; in addition, the basal piece bears a pair of ventral, articulated, subapical accessory lobes. The situation is further complicated in some groups by the addition of modified pregenital sclerites.

The few generalizations which will be made at this time concern the position of the tegmen (unknown in several groups) and the occurrence of accessory lobes on the paramere. The dorsal or "normal" orientation of the tegmen occurs in MYCP, TETR, PNTH, EUST, MLDR, ARCH, PERI, CHAL, DIAP, most TENB, EURY, PYTH, PYRO, OTHN?, TROG, AEGI, SALP, DACO, INOP, ANAS, SCRP, MACR, ANTH, and MELO. The ventral or "inverted" type occurs in PISN, MORD, PTER, SPHN, CIIN, MONM, COLY, ULOD, USEC, ZOPH, ZOLO, some TENB, PRST, NEMA, CEPH, STEN, CALO, OEDM, PEDL, SYNC, MYCT, HEMP, TRCT, ISCH, EUGL, and RHIP. The condition in some of these groups may be variable, as it is in the Tenebrionidae. Accessory lobes of a particular type, which are narrow and attached near the base of the single paramere, occur in BORI, TRCT, most PYTH, TROG, most SALP, DACO, and INOP. This has been used as evidence for uniting the salpingids and pythids, but it is obvious that more groups are involved (*see* Spilman 1952; 1967). The pterogeniid aedeagus is of the inverted type, with a large basal piece and single (though deeply emarginate) paramere; the tegmen resembles that of the colydiid *Aulonium*, but the complex median lobe is unique among the forms examined.

Larval Characters

Larval characters in the Heteromera have been even less precisely defined than those of the adult. The frontoclypeal suture in the larva is almost always absent, but it appears to be at least vaguely indicated in MLDR, ARCH, ZOPH, CALO, and the tenebrionids. The clypeal area may be considered to begin at a line drawn between the dorsal mandibular articulations. In some larvae, the apex of the clypeus is unpigmented, and the line where the pigment ends may be mistaken for the frontoclypeal suture.

The coronal and frontal sutures (epicranial suture) have been demonstrated to be ecdysial lines (Snodgrass 1960), and they are not usually associated with internal ridges (but see below). In the preceding descriptions, I have used epicranial stem for the basal portion of the line and frontal arms for the anterolateral branches. In most Heteromera, the frontal arms are lyriform and the epicranial stem is short or absent, but relatively long stems with lyriform arms occur in PISN, HALL, some EUST (*see* Hayashi 1975), PTER, CALO, SYNC, SCRP, and ANTH; the stem in pterogeniids is further distinguished by being bent to the left. Some Heteromera have straight V-shaped frontal arms, usually associated with a

long stem (most MLDR, SPHN, CIIN, some ZOPH, CHAL, ZOLO, DIAP, most TENB, NEMA, CEPH, OEDM and MELO). In a few groups (PTER, CHAL, ANAS), the two frontal arms are joined anteriorly by a transverse ecdysial line.

The head capsule may bear, in addition, one or two internal ridges, which have been called endocarinae. The term has usually been restricted to a median internal ridge which extends anteriorly from the epicranial stem, but here it will include those which coincide with the stem and sometimes extend onto the bases of the frontal arms (sutural), those median carinae which extend anterad of the stem (anterior), and those which lie laterad of the epicranial stem and/or frontal arms (lateral). A single sutural endocarina occurs in MORD, CIIN, ZOPH, DIAP, NEMA, CEPH, CALO, OEDM, and SYNC, while two sutural endocarinae occur in those forms without or with a very short stem (MLDR, OSPH?, EURY, PEDL, OTHN, TROG, AEGI, SALP, INOP). Lateral endocarinae are restricted to the Monommidae, while the anterior type occurs in some EUST, HEMP, SCRP, and ANTH.

The ventral part of the mouth cavity just above the labiomaxillary complex is strengthened by sclerotized hypostomal redges, which may continue posteriorly as hypostomal rods. These rods are usually divergent or subparallel and occur in many groups of Heteromera. They are absent in PNTH, MORD, SPHN, CIIN, ZOPH, PERI, CHAL, ZOLO, DIAP, TENB, NEMA, CEPH, OEDM, EURY, PEDL, SYNC, PYTH, AEGI, and SCRP, but may be quite short in some other groups. A second pair of ridges may extend posteriorly from the ventral mandibular articulations and lend further support to the ventral mouthparts; these structures, which have been called ventral epicranial ridges by Glen (1950), are common in Elateriformia, but occur within the Heteromera only in Ciidae and some Biphyllidae.

The malar apex of the maxilla is often used to compare heteromerous larvae, but the terminology is sometimes confusing. The word "uncus" has been used for a variety of structures at the inner apical angle, but it is sometimes restricted to a distinct lobe, such as that in *Anaspis*. The inner angle in many Heteromera bears one to several teeth, and this is called the uncus by Watt (1974a; 1974b) and Hayashi (1969; 1972). This type of uncus occurs in BYTU, BIPH, PTER, ARCH, MONM, COLY, USEC, ZOPH, PERI, PRST, NEMA, STEN?, CALO, OEDM, EURY, PEDL, SYNC, MYCT, BORI, PYTH, PYRO, OTHN, TROG, SALP, and INOP. The apex of the mala may also be cleft, so that it is partly divided into as inner and outer section; this cleft is usually associated with a sclerotized area and occurs in MONM, COLY, USEC, ZOPH, PERI, STEN?, CALO, OEDM, EURY, PEDL, SYNC, MYCT, HEMP, BORI, PYTH, PYRO, OTHN, TROG, and ANAS. In PRST, NEMA, and CEPH, there is a broad, shallow gap at the malar apex, which is not associated with a sclerotized area, and this may also be the case in TRCT (if the stylized drawing of Gahan, 1908, is to be belived). In PTER, there is a distinctive, bifurcate uncus near the inner angle (*see* Fig. 25); also unique are the dorsal, laciniar lobe in SPHN and CIIN, the dorsal brush of TETR and EUST, and the previously mentioned uncus of ANAS.

Recent studies with the scanning electron microscope have helped clarify the structure of the larval mandible and have revealed certain types

of microsculpture previously overlooked. The mandibular prostheca, common throughout the Clavicornia, is absent in almost all heteromerans. The term has been applied to a variety of structures, arising from the area lying between the apical teeth and the mola, most of which are hyaline or unpigmented and often flexible or membranous as well. Within the Heteromera, the Biphyllidae have a complex prostheca consisting of comb-like processes, while some byturids have vestiges of this. In the Ciidae, the mola is absent, and there is a small hyaline tooth in the molar area; this was called "retinaculum" by Lawrence (1971a; 1974) but has no relationship to the retinaculum in Adephaga or Elateridae. This type of hyaline tooth or several such teeth turn up in other heteromerans which have lost the molar part (MONM, BOTH, AEGI, some SALP, some INOP) and may be remnants of molar teeth.

In some primitive heteromerans (BIPH, MYCP, HALL, COLY), the molar region of the mandible is tuberculate, and the tubercles tend to be placed in transverse rows (perpendicular to the long axis of the mandible) and extend onto the ventral surface as well. The tubercles may also coalesce laterally, forming transverse ridges, alternating with deep troughs. In PISN, PTER, and ARCH, the entire surface appears to have been reinforced by the coalition of these tubercles, so that it consists of transverse ridges alternating with rows of small, deep pits (Figs. 16-23). Except for the biphyllids, these mandibles are somewhat asymmetrical with the right mola more oblique than the left, and in the pterogeniids the asymmetry is extreme. Large, asymmetrical mandibles with a molar surface consisting of fine transverse ridges, alternating with deep troughs, may be found in a number of derived heteromerans, such as SYNC, BORI, PYTH, PYRO, and OTHN, while in others (DIAP, PRST, NEMA, CEPH, CALO, and OEDM) the ridges are shallower and show no signs of a previous tuberculate condition. Within this latter group are forms with distinctly asymmetrical head capsules (DIAP, PRST, NEMA, OEDM; *see* Mamayev 1973). Mandibles with transverse ridges on the mola also occur in STEN, PEDL, some MYCT, HEMP, TRCT, TROG, some SALP, and some INOP, but the details of these have not been examined with the S.E.M. Two other major trends involve the gradual reduction of the mola in some lines and in others the formation of two concave molar areas which act in conjunction with a hypopharyngeal sclerome (*see* below) to compact food masses. Molar reduction is often thought to occur in association with predaceous habits, but it is just as likely to occur in those species which feed on particularly hard substrates. Molar reduction can be seen in BYTU, TETR, PNTH, EUST, MLDR, OSPH, MORD, SPHN, CIIN, MONM, some COLY, BOTH, PERI, AEGI, some SALP, some INOP, ANAS, SCRP, ANTH, EUGL, RHIP, and MELO. Following the details of these developments is beyond the scope of the present paper. A concave molar area occurs in ZOPH, CHAL, ZOLO, most TENB, EURY (with a few ridges), and some MYCT.

The hypopharyngeal sclerome usually refers to a distinctly sclerotized structure just behind the pypopharynx proper and attached to the mesal portion of the hypopharyngeal bracon (*see* Fig. 8). The structure is often mola-like, but is may consist of a sclerotized bar only, and it is often associated with various setal brushes. The mesal area of the bracon and the base of the mentum are often reinforced by a sclerotized ring, but I have

restricted the word sclerome to a sclerotized area on the floor of the mouth behind the hypopharynx. This structure may function in connection with ventral mandibular tubercles to cut food particles, or it may act in conjunction with the concave molar areas to compact food masses. A hypopharyngeal sclerome of some kind almost invariably occurs wherever the mola is developed, and it is lost in groups such as tetratomids, melandryids, ciids, monommids, and those salpingids and inopeplids which have undergone extreme molar reduction.

Scanning electron microscope studies have been particularly helpful in clarifying the structure and possible function of the dorsal mandibular armature. Shiny patches or vague lines on the basomesal portion of the dorsal mandibular surface may be seen with light microscopy, and such areas have been described by Hayashi (1975: 165) for *Synchroa*. As seen in Figs. 18-19 and 22-23, these areas contain fine, cuticular elements, usually flattened, which are inclined and which face in a basomesal direction; they may be packed in groups of three or four and form oblique rows extending from basolateral to apicomesal. These structures occur in a variety of Coleoptera (primitive staphylinoids, primitive dermestoids, many Cucujoidea) and apparently act in conjunction with fringed pharyngeal plates (Fig. 24) to move small particles into the mouth cavity (or conversely to keep these particles away from the membranes at the bases of the mandibles). Further studies on the structure of these and other parts of the larval feeding mechanism are nearing completion and will be published elsewhere. Dorsal mandibular armature has been observed in BIPH, MYCP, PISN, PTER, ARCH, COLY, PRST, NEMA, CEPH, CALO, OEDM, EURY, PEDL, SYNC, BORI, PYTH, PYRO, OTHN, TROG, some SALP, and some INOP, but the cuticular elements in PRST are restricted to a small area, while those of NEMA and CEPH are, in addition, more randomly arranged and not in distinct rows.

Characters involving the labium, maxillary base, and labiomaxillary articulating area have been used to a limited extent in Heteromera. The maxillary articulating area is usually well-developed, although reduced in Ciidae, and it may be divided into two distinct parts in certain groups, such as ZOPH, SYNC, and CEPH. Special attention has been given to the division of the cardo, but this has been misused by some authors. In many cases, the cardo is partly divided internally by a ridge, whereas in the Mycteridae there may be two distinct pigmented areas but no internal division; in neither case can the cardo be said to be divided. These and other labial and maxillary characters may be of use in determining relationships among the Heteromera, but not until the various conditions are more clearly defined.

Spiracular characters have also been limited to one or two simple dichotomies, but Watt (1974b) has recently shown spiracular details to be useful in clarifying subfamilial relationships within the Tenebrionidae. Many species of Heteromera have annular-biforous spiracles, although in some the accessory chambers are much smaller than the peritreme. Annular spiracles occur in OSPH, MORD, CIIN, BOTH, ZOPH, PERI, CHAL, ZOLO, DIAP, TENB, NEMA, CEPH, CALO, OEDM, EURY, SYNC, MYCT, BORI, TRCT, PYTH, PYRO, AEGI, INOP, SCRP, ANTH, EUGL, RHIP, and MELO, but in most of these cases, the condition is obviously derived from the annular-biforous type.

The abdominal apex (segments 9 and 10) exhibits considerable variation among the Heteromera and may prove useful in phylogenetic studies. The 10th segment is typically somewhat transverse, more or less membranous, and postero-ventrally oriented, but it ranges from being almost cylindrical and posterior (BYTU, BIPH, NEMA) to strongly transverse with distinct, lunate tergum and sternum (MYCO, ARCH, SCRP, EUGL), reduced and ventrally oriented (MYCT, BORI, PYTH, PYRO, SALP, etc.), or almost concealed by 9th segment, except for protruding pseudopods (ZOLO, TENB). The tergum of segment nine usually bears a pair of solid urogomphi, but these may be reduced or lost in various groups (MLDR, MORD, CIIN, CHAL, DIAP, TENB, NEMA, OEDM, etc.). In the pythid-salpingid group, the ninth tergum extends well onto the ventral surface, and may be divided into several plates, while in the Mycteridae and Boridae, it forms a hinged structure which articulates with segment 8 (and the enclosed 9th sternite and 10th segment). The ninth sternum often bears two or more teeth or asperities, which have been used as key characters. A single pair of basal asperities may be found in the larvae of HALL, PEDL, SYNC, TROG, AEGI, and most SALP. The number of basal asperities on each side is from 2 to 6 in INOP, 4 in CALO, 6? in TRCT, about 10 in OTHN and *Istrisia*, and about 14 in PYTH and PYRO. In a few taxa, asperities occur at the apex of the ninth sternum: a pair of fairly large teeth near the midline in EURY, and about 40 very small asperities along the apical edge in SPHN, COLY, and PRST.

Phylogenetic Relationships

The preceding is essentially a presentation of raw data, taken from direct observation, except in a very few cases where larvae were unavailable for study. I have not attempted to determine the plesiomorphic and apomorphic condition of each character state, since in most cases such a dichotomy does not exist, at least at this rather crude stage of analysis. Perhaps as the morphological characters are more precisely defined, a greater number of truly synapomorphic conditions may be discovered. Works, such as those of Abdullah (1973; 1974) do little to clarify the situation, since the dichotomies presented are arbitrary and oversimplified, if not irrelevant, and much of the information appears to be taken from the literature.

Given the data presented above, however, it ought to be possible to recognize some clusters within the Heteromera, which might eventually form the basis for a new classification. The most recent heteromeran phylogeny was proposed rather tentatively by Crowson (1966). Not commenting on the relationships of the Byturidae, Biphyllidae, Prostomidae, or Oedmeridae, Crowson suggested a heteromeran ancestral type similar to the Tetratomidae, giving rise initially to mycetophagids, tetratomids, ciids, and pterogeniids (the last two represented as sister groups). He then proposed a more advanced ancestral type with zopherid-like larvae and synchroid-like adults, which would give rise to four main lines: Synchroidae- Cephaloidae- Zopheridae- Monommidae- Colydiidae- Tenebrionidae; Melandryidae- Mordellidae- Scraptiidae- Rhipiphoridae; Pythidae- Pyrochroidae- Salpingidae- Mycteridae- Inopeplidae- Othniidae; and Anthicidae- Euglenidae- Meloidae. There appears to be strong evidence

supporting the pythid-salpingid group in the aedeagus, larval mandible, and larval abdominal apex. Crowson's Anthicidae is used in the broad sense to include eurygeniines and pedilines, which are probably better placed near the Pyrochroidae. Also the Scraptiidae appear to be more closely related to the anthicid-euglenid group (in the narrower sense); this is quite evident in the larvae, and is consistent with adult structure, if the wedge-like body form is considered to be a protective adaptation independently arrived at in mordellids. New larval descriptions of Tetratomidae and Melandryidae by Hayashi (1972; 1975) and Viedma (1966; 1971) have tended to blur the distinctions between Tetratominae and Eustrophinae, as well as between the Piseninae and Mycetophagidae, while emphasizing the isolated position of *Hallomenus* and *Mycetoma*, and that of the more advanced melandryines and osphyines. Crowson's synchroid-cephaloid-zopherid group seems consistent with larval characters, although the adults have diverged greatly in structure, representing two different life cycle strategies. The Tenebrionidae may well be derived from this group, and there are indications that both Oedemeridae and Prostomidae might belong here as well. The relationship between monommids and colydiids appears to be well grounded on both larval and adult characters, but it is easier to relate the two of them to archeocrypticids, mycetophagids and pisenines, than to the Tenebrionidae. Perhaps some of the similarities between colydiids and tenebrionids involve colydiid genera that are misplaced to begin with (tenebri nids or zopherids with reduced numbers of tarsal segments). The answer to this and other questions may be answered by J. C. Watt, who is completing his studies on the Zopheridae and on the phylogeny of the Heteromera as a whole.

The phylogenetic relationships of the Pterogeniidae are to be sought among the primitive Heteromera, as suggested by Crowson (1966) and Lawrence (1971a; 1974), while possible sister groups include the Piseninae, Ciidae, and Archeocrypticidae, all three of which share with the pterogeniids such characters as the lack of an internal extension on the procoxa, presence of a frontoclypeal suture in the adult, and subcubital fleck on the wing. The Ciidae are similar to pterogeniids in having an inverted aedeagus, divided subcubital fleck (Ciinae only), and characteristic larval antenna with a narrowly conical and very long sensory appendix. Also, the subapical lobe formed by the displacement of inner malar spines in the larva of pterogeniids could be homologous to the laciniar lobe in Ciidae. The ciid mala, however, is rounded, not truncate, and lacks an uncus, and the laciniar lobe is much more basal in position, being at the level of the palpifer. Ciid adults differ in having internally open procoxal cavities and lacking the securiform apex on the larval maxillary palp, and the larvae have V-shaped frontal arms and no mandibular mola.

The mandibular mola in larval Pterogeniidae is of a highly specialized, grinding type, but it is easily derived from that of either Archeocrypticidae or Piseninae (with transverse ridges alternating with deep pits). These, in turn, are derivable from a simpler, tuberculate type, such as that of Mycetophagidae. Pisenine adults resemble those of Pterogeniidae in having internally closed procoxal cavities and an inverted aedeagus (but of a unique type), and the larva is similar in general form and antennal structure. The subcubital fleck, however, is not divided, and the larval mala is short and rounded without an uncus.

Adult Archeocrypticidae have securiform maxillary palps, but have a double closure of the procoxal cavities, a dorsally oriented aedeagus, and an undivided subcubital fleck. Archeocrypticid larvae differ from pterogeniids and resemble Mycetophagidae in the slightly flattened form with a transverse, posteriorly oriented 10th segment; the larval mala, on the other hand, is truncate and at the inner angle bears a bifurcate uncus which appears to be homologous with the laterally displaced uncus of Pterogeniidae.

The larval and adult biology of pterogeniids (feeding in bracket fungi) is similar to that of both ciids and tetratomids, whereas the Archeocrypticidae (at least several New World *Enneboeus*) inhabit leaf litter and feed on rotten flowers and probably other types of decaying plant material. The ciids, in particular, have evolved the habit of boring into relatively hard and durable fruiting bodies—the same species that are utilized by pterogeniids—and yet they have evolved a very different mandibular type (lacking a mola) and malar apex (round with a laciniar lobe and no uncus). Archeocrypticids, with a different type of biology, have a similar, but less modified type of mandible and a similar malar apex.

The evidence is certainly not conclusive, but it suggests that Archeocrypticidae and Pterogeniidae are closely related families, and that both have affinities to Ciidae, Tetratomidae, and Mycetophagidae.

ACKNOWLEDGMENTS

LITERATURE CITED

ABDULLAH, M. 1973. Larvae of the families of Coleoptera. III. Heteromera, cucujoidea: a key to the world families including their distinguishing characters. Jour. Nat. Hist., 7:535-544.

————. 1974. Heteromera (Coleoptera): a key to the world families including their distinguishing characters in the adult stage. Jour. Nat. Hist., 8:49-59.

———— and A. ABDULLAH. 1968. The taxonomic position of *Lagrioida* with a proposed new tribe of the Eurygeniinae (Col., Anthicidae). Ent. Monthly Mag., 104:73-74.

ARNETT, R. H. 1968. The Beetles of the United States (A Manual for Identification). Ann Arbor, Mich., Amer. Ent. Inst., xii + 1112 p.

BÖVING, A. G. and F. C. CRAIGHEAD. 1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. Ent. Amer. (n.ser.), 11:1-351, 125 pls.

CANDEZE, E. 1861. Histoire des metamorphoses de quelques coleopteres exotiques. Mem. Soc. Roy. Sci. Liege, 16:325-410, 6 pls.

CASEY, T. L. 1889. Coleopterological notices. I. Ann. New York Acad. Sci., 5:39-198.

CROWSON, R. A. 1944. Further studies on the metendosternite in Coleoptera. Trans. Roy. Ent. Soc. London, 94:273-310, pls. 1-10.

————. 1955. The Natural Classification of the Families of Coleoptera. London, N. Lloyd. 187 p., 212 figs.

————. 1960. The phylogeny of Coleoptera. Ann. Rev. Ent., 5:111-134.

————. 1966. Observations on the constitution and subfamilies of the family Melandryidae. Eos, 41:507-513.

————. 1967. The natural classification of the families of Coleoptera. Addenda and corrigenda. Ent. Monthly Mag., 103:209-214.

DOYEN, J. T. 1972. Familial and subfamilial classification of the Tenebrionoidea (Coleoptera) and a revised generic classification of the Coniontini (Tentyriidae). Quaest. Ent., 8:357-376.

GAHAN, C. J. 1908. On the larvae of *Trictenotoma childreni* Gray, *Melittomma insulare* Fairm., *Dascillus cervinus* L. Trans. Ent. Soc. London, 1908:275-282.

GEBIEN, H. 1925. Die Tenebrioniden (Coleoptera) des indomalayischen Gebietes, unter Beruecksichtigung der benachbarten Faunen, VIII. Die Gattungen *Anisocara, Spiloscapha, Menimus, Labidocera,* und *Pentaphyllus.* Phillippine Jour. Sci., 28:101-128, 1 pl.

GLEN, R. 1950. Larvae of the elaterid beetles of the tribe Lepturoidini (Coleoptera: Elateridae). Smiths. Misc. Coll., 111(11):1-246.

HAYASHI, N. 1969. On the larvae of some species of small families of Cucujoidea in Japan (Coleoptera). Ins. Matsumurana Suppl. 7, 9 p., 4 pls.

————. 1972. On the larvae of some species of Colydiidae, Tetratomidae and Aderidae occurring in Japan (Coleoptera: Cucujoidea). Kontyu, 40(2):100-111.

————. 1975. On the larvae of Melandryidae (Coleoptera, Cucujoidea) and some related families occurring in Japan. Kontyu, 43(2):147-169.

HLAVAC, T. F. 1972. The prothorax of Coleoptera: origin, major features of variation. Psyche, 79(3):123-149.

————. 1975. The prothorax of Coleoptera (except Bostrichiformia-Cucujiformia). Bull. Mus. Comp. Zool., 147(4):137-183.

KASZAB, Z. 1964. The zoological results of Gy. Topal's collectings in South Argentina. 13. Coleoptera—Tenebrionidae. Ann. Hist-Nat. Mus. Nat. Hungarici, Pars Zool., 56:359-387.

LAWRENCE, J. F. 1971a. Revision of the North American Ciidae (Coleoptera). Bull. Mus. Comp. Zool., 142(5):419-522.

_____.1971b. The taxonomic position of the genus *Petria* Semenow (Coleoptera: Alleculidae). Breviora, No. 380, 9 p.

_____. 1974. The larva of *Sphindocis denticollis* Fall and a new subfamily of Ciidae (Coleoptera: Heteromera). Breviora, No. 424, 14 p.

MAMAYEV, B. M. 1973. The morphology of the larva of the beetle genus *Nematoplus* Lec. and the phylogenetic connections of some families of Heteromera. Ent. Rev., 52(3):388-395 [translation].

MOTSCHULSKY, V. DE. 1858. Insectes des Indes orientales. 1:iere Serie. Etudes Ent., 7:20-122, 1 pl.

PASCOE, F. P. 1866. Longicornia Malayana . . . Trans. Ent. Soc. London, Ser. 3, 3:1-712, pls. 1-24.

PIC, M. 1937. Deux nouveaux Coleopteres de Java. Tijdschr. Ent., 80:304.

PONOMARENKO, A. G. 1973. The nomenclature of wing venation in beetles (Coleoptera). Ent. Rev., 51(4):454-458 [translation].

SEN GUPTA, T. and R. A. CROWSON. 1971. A review of the classification of the family Languriidae (Coleoptera: Clavicornia) and the place of Languriidae in the natural system of Clavicornia. Mem. Zool. Surv. India, 15(2):1-42.

SNODGRASS, R. E. 1960. Facts and theories concerning the insect head. Smiths. Misc. Coll., 142(1):1-61.

SPILMAN, T. J. 1952. The male genitalia of the Nearctic Salpingidae. Coleopt. Bull., 6:9-13.

_____. 1967. The heteromerous intertidal beetles (Coleoptera: Salpingidae: Aegialitinae). Pacific Ins., 9:1-21, 44 figs.

VIEDMA, M. G. DE. 1966. Contribucion al conocimiento de las larvas de Melandryidae de Europa (Coleoptera). Eos, 41:483-506.

_____. 1971. Redescripcion de la larva de *Eustrophinus bicolor* y consideraciones acerca de la posicion sistematica del genero *Eustrophinus* (Col. Melandryidae). Ann. Soc. Ent. France, N.S., 7(3):729-733.

WATT, J. C. 1967. The families Perimylopidae and Dacoderidae (Coleoptera, Heteromera). Proc. Roy. Ent. Soc. London, Ser. B, 36(7-8):109-118.

_____. 1974a. Chalcodryidae: A new family of heteromerous beetles (Coleoptera: Tenebrionoidea). Jour. Roy. Soc. New Zealand, 4:19-38, 45 figs.

_____. 1974b. A revised subfamily classification of Tenebrionidae (Coleoptera). New Zealand Jour. Zool., 1(4):381-452, 97 figs.